ANALYSIS OF FRESHWATER INFLOW EFFECTS ON METABOLIC STRESSES OF SOUTH TEXAS BAY AND ESTUARINE FISHES: STUDIES ON SMALL FISHES

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FINAL REPORT

to

TEXAS DEPARTMENT OF WATER RESOURCES

for

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ANALYSIS OF FRESHWATER INFLOW EFFECTS ON METABOLIC STRESSES OF SOUTH TEXAS BAY AND ESTUARINE FISHES: STUDIES ON SMALL FISHES

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EXECUTIVE SUMMARY -- RECOMMENDATIONS

Texas Department of Water Resources, Interagency Cooperation Contract No. IAC (77-78)-0866, TWDR Contract No. 14-80017.

This report deals with continuing studies on the investigation of freshwater inflow effects on South Texas estuaries and bays by (a) utilizing fish as indicators of optimal effects of these inflows and (b) assessing the metabolic performances of fishes in a variety of salinity situations as an analytical tool independent of fishery and pollution effects. The current study at 15°C deals with the juvenile stages of Atlantic croaker, red drum and spotted seatrout, and compares metabolic performance of the juveniles with that of their adult counterparts.

The metabolic scopes for activity of the spotted seatrout juveniles tend to be at an optimum around 20-30 ppt salinity, and at about 20 ppt for both Atlantic croaker and red drum juveniles. The scopes drop off toward 10 ppt and beyond 30 ppt for all three species.

The patterns of the scope-salinity curves are about the same as for the adults, except that they are more upwardly displaced and are spread out flatter to indicate a broader, more euryhaline response on the part of the juveniles.

The upward displacement of the scope curves for juveniles also is a straightforward indication that they grow much more rapidly than adults.

Each curve tends to be related to the general natural history information on both growth rate and degree of salinity tolerance known for the individual species. Thus Atlantic croaker,

red drum, and spotted seatrout are decreasingly euryhaline.

Several recommendations and suggestions follow:

The shapes of the metabolic scope-salinity response curves at 15°C are sufficiently different between species and between adults and juveniles (refer to Figure 18 in text) to suggest that extrapolation should be avoided.

Similar curves should ultimately be drawn up for additional, important species and for higher summer temperatures above 25°C.

Because the scope-salinity curves for juveniles indicate that they are more euryhaline than adults, great care should be used in future stress experiments (or interpretation of stress effects) so that the more vulnerable adults are protected. These findings also indicate that very old and large adults need to be investigated for possible increasing vulnerability to salinity changes.

The time course of metabolic (or other) response to salinity changes should be investigated. (This investigation has been planned for the 1979-80 fiscal year) and a report is being prepared.

Small fish especially are metabolically very sensitive to poor "condition" (which means that slight stresses of any kind cause fish to be emaciated). For all future experiments and direct environmental assessments of the well being of fishes, it is recommended that their weight-length condition be quantitatively enumerated before any interpretations of the data are made.

It is suggested that further observations be made to examine the rather frequent recurrence of metabolic, growth, or condition, depression that occurs at about 30 ppt.

Finally, it is suggested that the types of metabolic scope

assessments utilized in this and previous salinity studies, be developed for assessment of general water quality conditions to detect even the slightest levels of sublethal pollution.

INTRODUCTION

The purpose of this study is to extend previous studies of the effects of freshwater influxes on subadult to adult Texas coastal fishes for the evaluation of similar effects on the fingerling to juvenile stages of the same species. Previous studies with the larger fishes, referred to as the 1975 short-term pilot study, the 1975-76 study of routine metabolism for several types of bay waters (Wohlschlag, 1976), and the 1976-77 study of active metabolism for several species (Wohlschlag, 1977), all indicated that there was little shift in optimal salinity with temperature and that about 20-25 ppt salinity was optimal for the several species investigated. For the spotted seatrout (Wohlschlag and Wakeman 1978) the respiratory metabolism for maximum sustained swimming activities is at a maximum at around 20 ppt salinity, while the maintenance (standard) metabolism is minimal at about the same salinity. The scope for activity, or simply scope, is the difference between the metabolic levels of standard or maintenance and of maximum sustained activity.

The scope concept was originally suggest by Fry (1947) and has proved to be quite seminal (Fry 1957, 1971), with applications ranging from comparisons of selective evolutionary advantages among ectotherms and endotherms (Bennett and Ruben 1979), to zoogeographical and salinity delineations on the distribution of a fish (Wohlschlag and Wakeman 1978), and to the assessment of toxicity of ocean-dumped industrial wastes (Wohlschlag and Parker, In Press). In general terms, the scope is maximal under minimal environmental stress. With any additional stress, scope tends to decrease, because either the active metabolism decreases

or the standard metabolism increases, or both. The property of a decrease in metabolic scope in direct proportion to environmental stress provides the basis for evaluation of departures from optimal salinities in this study.

In a similar manner as optimal salinity at maximal scope occurs in the above studies, so does the optimal salinity generally occur with maximum swimming performance. Swimming performance without metabolic measurements has already been suggested as a direct measure of salinity optimality in earlier studies of this TWDB/TDWR series.

The use of metabolic scope in this study, in contract to earlier studies on Gulf estuarine fishes at subadult to adult sizes, is for the express purpose of extending the size range to lower size ranges from about 4-5 cm up to about 20 cm. This is the size range when the fish tend to school persistently, feed intensively and grow rapidly. It is also a size range over which both the fish and their preferred food organisms could be influenced adversely by salinity and other environmental variables at less than optimal conditions. At very early egg to post larval stages, the salinity, temperature and other variables are expected to be rather rigidly defined for most species by simple measurements in the environments at the times and places of spawning, which are fairly easily recognizable. However, salinity requirements during the time period, which follows shortly after hatching until the various coastal and estuarine fishes are actually taken in sports or commercial catches at times and localities of known salinities, are relatively poorly known for life history information in general and the nature of

stresses in various coastal salinity regimes in particular. It is possible that the smaller fish would be more resilient to stresses as was the case for the small pinfish subjected to sublethal petrochemical pollutant levels, whereby the metabolic depression at temperature extremes was much less than for the larger pinfish (Wohlschlag and Cameron, 1967).

With this life history information gap in mind and the establishment of metabolically optimal salinities of about 20-25 ppt for spotted seatrout, red drum, black drum, Atlantic croaker, etc. in the subadult to adult sizes, the purpose of this study is to determine whether the smaller members of some of these species adjust to a range of salinities different from larger members.

METHODS AND MATERIALS

Preliminary Procedures

The fish used in this study were: red drum, Sciaenops ocellata; spotted seatrout, Cynoscion nebulosus; and Atlantic croaker, Micropogon undulatus. Attempts to use the black drum, Pogonias cromis, were discontinued when fingerlings became unavailable.

All the fish utilized in the experiments were postlarval and underyearling. The 5-20 cm size range was unavoidable due to their rapid and seasonal growth rates. The fish were captured by use of seines, and occasionally by trawls, with small meshed (1/4-inch) netting in the Port Aransas area. Shortly after capture, the fish were transferred to large laboratory holding tanks where temperatures and salinities were near ambient environmental levels for initial acclimation.

If the temperature of the holding tanks was more than 3°C different from a desired experimental temperature, the fish would be acclimated in one of two ways:

(1) The experimental tank would be filled from the same water supply that fed the holding tanks. Then the fish could be transferred to the experimental tank and the temperature gradually changed over 24-48 hours to the experimental temperature of 15±0.1°C. The salinity would then be adjusted to the desired level by addition of either de-ionized water or commercial sea salts.

(2) If the experimental tanks were already at a suitable temperature and salinity, new fish could be placed in 20 l containers floated on the water surface of the experimental tank. The 20 l containers would be filled with holding tank water, which would gradually equilibrate to 15°C. At this stage, salinity could be adjusted within the 20 l container by gradual displacement with water from the experimental tank.

All salinity changes were held to 5 ppt per day. Fish were acclimated at least two days at final salinities of 10, 20, 30, 40 ppt (± 0.5 ppt) and at 15°C, during which time fish were normally fed at least every other day. Food consisted of small live shrimp or mullet fry when available. Otherwise chopped fish, squid or shrimp were used. Daily feeding was ordinarily too often for best survival.

Because of the relatively high respiratory metabolism of small fish, the experimental fish were fasted for only 24 hr prior to metabolic rate determinations.

Respiratory Metabolism

Resting Rates. Oxygen consumption rates were measured either in stoppered 2.87 l Fernbach flasks or in the 207 l Blazka chamber at zero velocity for several hours (Wohlschlag and Wakeman 1978). The Fernbach flasks were submerged in one of the experimental tanks used for acclimation and were covered with a black plastic shield. Fish were placed in the aerated flasks overnight for acclimatization. At the initiation of an experiment, aeration was discontinued and the fish were sealed

in the flask with a rubber stopper through which a syringe needle could be inserted for water sampling. In the 207 l Blazka chamber the fish, usually in small schools, were left for several hours to overnight in order to have a sufficient amount of oxygen consumed for precise detection; in the 2.87 l Fernbach flasks, retention for about one-half hour to several hours, depending on size, was usually sufficient for adequate precision in rate determinations.

Active Rates. The techniques for measuring the active rates with the Blazka chamber have been described in earlier reports to the Texas Department of Water Resources and in Wohlschlag and Wakeman (1978) for single fish. Because of the volume of the chamber and the small size of the fish, small schools were placed in the chamber so that 1-3h would be required for sufficiently precise oxygen consumption rate determinations. In determining the maximum swimming speed for adult fish of these species, the transition from the sustained level to burst speeds was acute. But the normal mode of swimming of the juveniles seemed to incorporate some aspects of burst swimming and to be much more erratic than for the subadults to adults. Because of the somewhat erratic swimming performances of the groups of juveniles, the method finally adopted was to increase the impeller speed until the tail beat frequency was greater than 5 complete oscillations per second. At that swimming rate the increases were at 2 cm sec^{-1} each 5 min until fish obviously could not maintain their positions as would be obvious when

being swept against the screen after first exhibiting erratic swimming activity. When erratic swimming was first observed, the speed was reduced 2 cm sec^{-1} and oxygen consumption rate determinations begun. If the fish could not maintain the speed, the experiment was aborted. The speed was then reduced still further until a speed that could be maintained for 1-3h was reached. For most of the groups, oxygen consumption rates were also determined at intermediate swimming rates, as well as at zero rates for estimating standard rates.

Regression Calculations

The multiple regression calculation procedures have followed those utilized in previous reports to the Texas Department of Water Resources and in Wohlschlag and Wakeman (1978). Modifications were required for utilizing data on groups of fish swimming in schools. Essentially the regressions are:

$$\hat{Y} = a + b_w X_w + b_v X_v + b_s X_s + b_{ss} X_s^2,$$

or

$$\hat{Y}_{kg} = a' + b_v X_v + b_s X_s + b_{ss} X_s^2,$$

where

$\hat{Y}$ = expected rate of O_2 consumption in $\log_{10} mgO_2 h^{-1}$;

$\hat{Y}_{kg}$ = expected metabolic rate in $\log_{10} mgO_2 kg^{-1} h^{-1}$;

a = constant;

X_w, X_v, X_s, X_{ss} are the independent variables, respectively, for $\log_{10}$ weight in grams, velocity in square root of total length per second ($L^{0.5} s^{-1}$); salinity in ppt, and salinity squared;

and

b_w, b_v, b_s and b_{ss} are the respective partial regression coefficients.

This is the same procedure used by Wohlschlag and Juliano (1959), Wohlschlag and Cameron (1967), Wohlschlag and Cech (1970), Wohlschlag and Wakeman (1978) and others. Regression techniques are in most statistical manuals, e.g., Snedecor and Cochran (1967) and in a variety of pretested library computer routines.

When the size ranges of fish in the groups were excessive and swimming behavior and performance were often erratic, an arbitrary attempt was made to "edit" the data by eliminating excessive length variability. For each group of fish in any experiment, the range in total length was noted. The range was expressed as a percentage of the total length of the largest fish in the group. The mean length range was then calculated for each species over all the experiments. Data based on groups of fish whose range of total lengths was greater than the mean were eliminated before the regressions were calculated. These regressions are referred to as "edited."

Scope Calculations

Scope for activity was determined in several ways at each of the 10, 20, 30 and 40 ppt salinity levels. The simplest system was to select the single maximum and minimum values observed at each salinity for each of the three species. The second system was to utilize the averages of the metabolic rates of fish which swam at maximum sustained rates and the averages of those fish whose metabolic rates were determined under resting conditions.

It was also considered useful to calculate metabolic rates at average maximum and zero swimming rates from the multiple regressions at average weights. (There was little difference between the regressions that used all the data and the "edited" regressions that were based on the data which excluded groups with excessive length variability among the individual fish.)

To take into account the fact that fish in poor condition have very low metabolic rates (Wohlschlag and Wakeman 1978), the coefficient of condition was calculated for some of the fish whose metabolism seemed suspiciously low. To this end, the weight to length coefficients were calculated for the fish of each salinity group. From the coefficients that were less than those reported in the literature for healthy fish, an upward adjustment of weight (hence metabolism) was possible from log weight on log log length regressions of the fish within the different salinity groups. If the ratios of coefficients were unity no adjustment in weight was made; if the expected-to-observed ratio was over unity, an upward adjustment was made.

Juvenile-Adult Comparisons

Because one of the major aspects of this study involves the salinity stresses that young fishes experience in South Texas coastal waters in comparison to what their adult counterparts experience, data on adults from earlier 1976-77 TWDB studies were reevaluated at 15°C insofar as possible and pertinent. Extrapolations were from existing adult metabolic data to 15°C and to swimming velocities at that temperature,

if data at 15°C were not otherwise available at each salinity.

Red drum. Data from Table 3, Table 3A, the regression equations 3A, 3B on p. 67, and Figs. 5 and 10 of the 1977 report provided the basic data. Both active and standard data were extrapolated and the scope recalculated at 15°C.

Atlantic croaker. The data from Tables 4, 4A regression equations 4A, 4B (p. 68) and Figs. 6 and 11 of the 1977 report furnished a basis for the extrapolations to 15° of the active and standard rates and the corresponding scope for activity.

RESULTS

Resting Metabolic Rates

The data in Tables 1, 2 and 3 are for the red drum, Atlantic croaker and spotted seatrout, respectively. These resting oxygen consumption rate measurements are for single fish in the Fernbach flasks and for groups of fish in the Blazka chamber. For the fish in groups, the average total length (TL) and the log of the average weight were used.

Swimming and Active Metabolic Rates

Oxygen consumption rate data for swimming red drum, Atlantic croaker and spotted seatrout are, respectively, in Tables 4, 5 and 6. In these three tables the groups that swam at maximum sustained rates are indicated by asterisks at each salinity level; two asterisks indicate the highest single rate.

Separate plots of portions of these data to assess the degree of variability at each salinity, as well as separate tabulations

Table 1. Red drum. Oxygen consumption rate data at resting conditions and 15°C.

Date	Salinity ppt	No. of Fish	Total Length (cm)	Log Wt. (g)	Log Ave. Wt.	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
Fernbach Flask Data:							
5 VII	40	1	12.0	1.2553	-	0.4788	2.2235
5 VII	40	1	12.0	1.2553	-	0.3529	2.0976
5 VII	40	1	12.0	1.2553	-	0.5208	2.2655
6 VII	40	1	17.8	1.7882	-	1.0952	2.3071
6 VII	40	1	18.4	1.8062	-	1.0729	2.2667
6 VII	40	1	18.4	1.8062	-	1.1325	2.3263
7 VII	40	1	14.7	1.2430	-	0.5104	2.2674
19 VII	20	1	17.0	1.6767	-	0.7655	2.0888
19 VII	20	1	17.0	1.6767	-	0.7278	2.0512
19 VII	20	1	17.0	1.6767	-	0.7355	2.0588
19 VII	20	1	12.6	1.3617	-	0.4434	2.0817
19 VII	20	1	12.6	1.3617	-	0.4434	2.0817
19 VII	20	1	12.6	1.3617	-	0.3854	2.0237
19 VII	20	1	12.6	1.3617	-	0.4803	2.1186
19 VII	20	1	13.2	1.3010	-	0.4434	2.1424
19 VII	20	1	13.2	1.3010	-	0.3397	2.0386
19 VII	20	1	13.2	1.3010	-	0.3397	2.0386
19 VII	20	1	13.2	1.3010	-	0.3677	2.0667
24 VII	10	1	12.5	1.2788	-	0.3940	2.1153
24 VII	10	1	12.5	1.2788	-	0.3815	2.1028

Table 1 (cont.)

Date	Salinity ppt	No. of Fish	Total Length (cm)	Log Wt. (g)	Log Ave. Wt.	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
24 VII	10	1	12.5	1.2788	-	1.3729	2.0941
24 VII	10	1	11.2	1.1139	-	0.2177	2.1038
24 VII	10	1	11.2	1.1139	-	0.3148	2.2009
24 VII	10	1	11.2	1.1139	-	0.1899	2.0759
24 VII	10	1	11.2	1.1139	-	0.2355	2.1216
24 VII	10	1	13.4	1.3802	-	0.4116	2.0314
24 VII	10	1	13.4	1.3802	-	0.5112	2.1310
24 VII	10	1	13.4	1.3802	-	0.5780	2.1978
Blazka Respirometer Data at Zero Velocity and Average Total Length and Weights:							
31 III	20	16	5.0	1.5051	0.3010	0.5516	2.0465
10 IV	20	1	14.2	1.4472	-	0.5855	2.1383
12 IV	20	4	9.7	1.5563	0.9542	0.7709	2.2146
18 IV	20	6	10.9	1.8837	1.1055	0.9750	2.0913
19 IV	20	4	13.3	1.9542	1.3522	1.0963	2.1421
22 IV	10	4	13.3	1.9420	1.3399	1.1642	2.2222
23 V	10	1	19.9	1.8976	-	1.1399	2.2423
24 VI	30	5	12.8	2.0170	1.3181	1.2785	2.2615
27 VI	30	5	12.5	1.9494	1.2504	1.1502	2.2009
28 VI	40	5	14.4	2.1746	1.4757	1.2876	2.1129

Table 2. Atlantic croaker. Oxygen consumption rate data at resting conditions and 15°C.

Date	Salinity ppt	No. of Fish	Total Length (cm)	Log Wt. (g)	Log Ave. Wt.	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
Fernbach Flask Data:							
10 II	30	1	13.3	1.3979	-	0.6377	2.2398
10 II	30	1	13.3	1.3979	-	0.6212	2.2232
15 II	30	1	13.1	1.2788	-	0.5350	2.2562
15 II	30	1	13.1	1.2788	-	0.5253	2.2465
15 II	30	1	13.1	1.2788	-	0.4962	2.2175
16 II	30	1	17.4	1.7404	-	0.9610	2.2206
Blazka Respirometer Data at Zero Velocity and Average Total Lengths and Weights:							
8 III	40	4	16.2	2.2753	1.6733	1.5193	2.2440
20 III	40	3	16.7	2.1553	1.6782	1.3259	2.1706
22 III	40	2	17.0	2.0086	1.7076	1.1642	2.1556
27 III	20	3	17.2	2.2455	1.7684	1.3163	2.0708
30 III	20	3	17.3	2.2227	1.7459	1.0442	1.8215
15 IV	20	4	14.4	2.1189	1.5169	1.1923	2.0734
1 VI	10	2	16.0	1.9112	1.6101	1.1231	2.2119
6 VI	10	3	15.5	2.0453	1.5682	1.2208	2.1755

Table 3. Spotted seatrout. Oxygen consumption rate data at resting conditions and 15°C.

Date	Salinity ppt	No.of Fish	Total Length (cm)	Log Wt. (g)	Log Ave. Wt.	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
Fernbach Flask Data:							
3 VII	40	1	10.2	0.9031		0.1464	2.2433
3 VII	40	1	10.2	0.0031		0.1389	2.2358
5 VII	40	1	14.2	1.4624		0.7338	2.2714
5 VII	40	1	14.2	1.4624		0.6522	2.1898
5 VII	40	1	14.0	1.4314		0.6732	2.2418
5 VII	40	1	14.0	1.4314		0.6684	2.2370
6 VII	40	1	16.2	1.5315		0.7896	2.2582
6 VII	40	1	11.2	1.2041		0.4467	2.2425
6 VII	40	1	11.2	1.2041		0.4260	2.2219
7 VII	40	1	10.1	0.9542		0.1219	2.1676
7 VII	40	1	10.1	0.9542		0.2704	2.3162
7 VII	40	1	10.1	0.9542		0.2076	2.2533
7 VII	40	1	10.1	0.9542		0.2357	2.2815
13 VII	30	1	13.4	1.3010		0.5051	2.2041
13 VII	30	1	13.4	1.3010		0.5630	2.2620
13 VII	30	1	13.4	1.3010		0.5310	2.2299
13 VII	30	1	12.6	1.900		0.4380	2.1480
13 VII	30	1	12.6	1.2900		0.3714	2.0812
13 VII	30	1	12.6	1.2900		0.5051	2.2151

Table 3. (Con't)

Date	Salinity	No.of Fish	Total Length (cm)	Log Wt. (g)	Log Ave. Wt.	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
Blazka Respirometer Data at Zero Velocity and Average Total Lengths and Weights:							
13 II	30	3	12.8	1.6628	1.1856	0.8633	2.2006
9 VI	10	5	12.6	1.9138	1.2148	1.0159	3.1021
10 VI	10	2	17.5	1.9269	1.6258	1.0980	2.1711
12 VI	10	5	12.6	1.9138	1.3148	1.0658	2.1520
13 VI	10	2	17.5	1.9269	1.6258	1.0739	2.1471
13 VI	10	2	17.5	1.9269	1.6258	1.0813	2.1544
16 VI	20	4	10.7	1.6435	1.0414	0.8654	2.2219
19 VI	20	2	17.5	1.9139	1.6128	0.9204	2.0086
20 VI	20	6	12.1	1.9243	1.1461	1.0478	2.1235

Table 4. Red drum. Oxygen consumption rate data at various swimming rates in Blazka chamber at 15°C. Single asterisks denote maximum sustained rates; double asterisks denote single highest rate at each salinity interval.

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
31 III	20	16	5.0	0.3010	6.5	0.9802	2.4751*
7 IV	20	7	7.9	0.7404	5.1	1.1765	2.5911
7 IV	20	7	7.9	0.7404	8.0	1.2301	2.6446
10 IV	20	8	8.9	0.8858	5.5	1.3016	2.5127
10 IV	20	8	8.9	0.8858	8.2	1.3403	2.5514
10 IV	20	8	8.9	1.7889	9.6	1.3683	2.5794*
11 IV	20	1	14.2	-	3.3	0.8912	2.4440
11 IV	20	1	14.2	-	10.9	1.0393	2.5922
11 IV	20	1	14.2	-	15.2	1.1612	2.7141**
12 IV	20	4	9.7	0.9542	7.3	1.0326	2.4763
12 IV	20	4	9.7	0.9542	9.2	1.1370	2.5807
18 IV	20	6	10.9	1.1055	6.2	1.2300	2.3464
18 IV	20	6	10.9	1.1055	9.9	1.3869	2.5032
19 IV	20	4	13.3	1.3522	6.7	1.4354	2.4812
19 IV	20	4	13.3	1.3522	10.2	1.4563	2.5020
19 IV	20	4	13.3	1.3522	14.1	1.5603	2.6061*
22 V	10	4	13.3	1.3399	7.9	1.2771	2.3351
22 V	10	4	13.3	1.3399	9.0	1.3289	2.3869
22 V	10	4	13.3	1.3399	11.8	1.5473	2.6053*
23 V	10	1	19.9	-	5.6	1.3277	2.4301

Table 4 (cont.)

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
23 V	10	1	19.9	-	8.7	1.4195	2.5219
23 V	10	1	19.9	-	11.5	1.4739	2.5762*
23 V	10	1	19.9	-	7.4	1.3599	2.4622
23 V	10	1	19.9	-	10.6	1.4631	2.5655*
25 V	10	5	14.5	1.5263	7.0	1.6500	2.4247
25 V	10	5	14.5	1.5263	10.8	1.7468	2.5215*
30 V	10	5	13.6	1.4183	5.6	1.5361	2.4188
30 V	10	5	13.6	1.4183	8.9	1.6030	2.4857
30 V	10	5	13.6	1.4183	12.2	1.7749	2.6576**
30 V	10	5	13.6	1.4183	12.2	1.7169	2.5997*
23 VI	30	6	12.7	1.2904	7.5	1.6702	2.6021
23 VI	30	6	12.7	1.2904	10.4	1.5972	2.5290
23 VI	30	6	12.7	1.2904	10.9	1.6228	2.5546*
23 VI	30	6	12.7	1.2904	5.8	1.4435	2.3753
24 VI	30	5	12.8	1.3181	5.7	1.4670	2.4499
24 VI	30	5	12.8	1.3181	12.0	1.7052	2.6882*
26 VI	30	5	15.2	1.5224	7.9	1.7128	2.4914
26 VI	30	5	15.2	1.5224	11.6	1.8861	2.6646*
26 VI	30	5	15.2	1.5224	7.9	1.7156	2.4942
26 VI	30	5	15.2	1.5224	11.6	1.8861	2.6646*
27 VI	30	5	12.5	1.2504	5.8	1.5181	2.5687

Table 4 (cont.)

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
27 VI	30	5	12.5	1.2504	11.6	1.6254	2.6760*
27 VI	30	5	12.5	1.2504	7.6	1.4768	2.5274
27 VI	30	5	12.5	1.2504	11.0	1.6430	2.6936*
27 VI	30	5	12.5	1.2504	8.1	1.4389	2.4895
27 VI	30	5	12.5	1.2504	11.0	1.5639	2.6145**
28 VI	40	5	14.4	1.4757	6.5	1.7622	2.5876
28 VI	40	5	14.4	1.4757	9.7	1.8426	2.6679
28 VI	40	5	14.4	1.4757	5.4	1.6602	2.4856
28 VI	40	5	14.4	1.4757	7.6	1.6959	2.5213
28 VI	40	5	14.4	1.4757	9.7	1.8305	2.6559*
28 VI	40	5	14.4	1.4757	9.7	1.8098	2.6325*
29 VI	40	5	12.0	1.2304	7.1	1.4795	2.5501
29 VI	40	5	12.0	1.2304	8.9	1.4273	2.4979
29 VI	40	5	12.0	1.2304	10.7	1.6059	2.6765*
29 VI	40	5	13.6	1.3747	5.6	1.5430	2.4692
29 VI	40	5	13.6	1.3747	8.9	1.7085	2.6348
29 VI	40	5	13.6	1.3747	10.0	1.7085	2.6348*
29 VI	40	5	13.6	1.3747	6.7	1.5820	2.5083
30 VI	40	4	15.4	1.5502	6.3	1.6959	2.5436
30 VI	40	4	15.4	1.5502	12.5	1.8386	2.6863*
30 VI	40	4	15.4	1.5502	8.4	1.5497	2.3974
30 VI	40	4	15.4	1.5502	12.5	1.8507	2.6984**

Table 5. Atlantic croaker. Oxygen consumption rate data at various swimming rates in Blazka chamber at 15°C. Single asterisks denote maximum sustained rates; double asterisks denote single highest rate at each salinity interval.

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
7 II	30	4	15.5	1.6284	12.5	1.2911	2.6678*
7 II	30	4	15.5	1.6284	6.2	1.0011	2.3779
7 II	30	4	15.5	1.6284	7.3	0.9900	2.3668
10 II	30	2	15.0	1.6101	6.4	1.4018	2.4907
10 II	30	2	15.0	1.6101	10.6	1.5559	2.6447**
15 II	30	4	13.2	1.4087	11.3	1.5669	2.5562*
15 II	30	4	13.2	1.4087	6.8	1.4842	2.4735
16 II	30	3	16.5	1.7019	7.1	1.7320	2.5530
16 II	30	3	16.5	1.7019	10.1	1.7636	2.5847*
16 II	30	3	16.5	1.7019	6.1	1.3668	2.1878
8 III	40	4	16.2	1.6733	9.2	1.8054	2.5300*
9 III	40	5	12.7	1.2355	5.8	1.4125	2.4780
9 III	40	5	12.7	1.2355	8.1	1.5166	2.5820
9 III	40	5	12.7	1.2355	12.7	1.5020	2.6475*
9 III	40	6	12.2	1.3010	8.2	1.7416	2.6625
9 III	40	6	12.2	1.3010	13.5	1.7320	2.6528**
20 III	40	3	16.7	1.6782	9.0	1.5140	2.3587
20 III	40	3	16.7	1.6782	12.6	1.4978	2.3424*
21 III	40	6	12.2	1.3028	5.9	1.6501	2.5691
21 III	40	6	12.2	1.3028	9.4	1.5753	2.4943
21 III	40	6	12.2	1.3028	12.9	1.7106	2.6296*

Table 5 (cont.)

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
22 III	40	2	17.0	1.7076	7.0	1.3260	2.3174
22 III	40	2	17.0	1.7076	12.9	1.5371	2.5289*
22 III	40	2	17.0	1.7076	8.9	1.5028	2.4941
27 III	20	3	17.2	1.7684	6.9	0.9898	1.7443
27 III	20	3	17.2	1.7684	10.9	1.3448	2.0993
27 III	20	3	17.2	1.7684	16.3	1.8777	2.6322**
28 III	20	5	12.8	1.4133	6.3	1.8041	2.6918
30 III	20	3	17.3	1.7459	8.4	1.6114	2.3886
30 III	20	3	17.3	1.7459	13.8	1.5568	2.3341*
3 IV	20	3	17.2	1.7559	7.4	1.6094	2.3764
3 IV	20	3	17.2	1.7559	12.9	1.8134	2.5804*
5 IV	20	4	14.4	1.5169	7.6	1.3104	2.1915
5 IV	20	4	14.4	1.5169	14.0	1.6316	2.5127*
23 V	40	5	13.8	1.4425	6.9	1.3304	2.1889
23 V	40	5	13.8	1.4425	11.0	1.4917	2.3502*
31 V	10	11	8.3	0.8562	5.7	1.3104	2.4128
31 V	10	11	8.3	0.8562	8.5	1.3745	2.4768*
1 VI	10	2	16.0	1.6101	7.2	1.3278	2.4166
1 VI	10	2	16.0	1.6101	12.8	1.5496	2.6385**
2 VI	10	2	17.9	1.8028	7.3	1.4915	2.3877
2 VI	10	2	17.9	1.8028	9.7	1.6219	2.5181
2 VI	10	2	17.9	1.8028	14.5	1.7143	2.6104*

Table 5 (cont.)

Date	Salinity ppt	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
6 VI	10	3	15.5	1.5682	7.8	1.4382	2.3929
6 VI	10	3	15.5	1.5682	10.9	1.5931	2.5478
6 VI	10	3	15.5	1.5682	13.5	1.6414	2.5960*

Table 6. Spotted seatrout. Oxygen consumption rate data at various swimming rates in Blazka chamber at 15°C. Single asterisks denote maximum sustained rates, double asterisks denote single highest rate at each salinity interval.

Date	Salinity (ppt)	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-1}$
06 II	30	3	13.5	1.2937	6.1	1.1471	2.3762
06 II	30	3	13.5	1.2937	8.8	1.3605	2.5895*
08 II	30	5	11.6	1.1271	8.4	1.4969	2.6708
08 II	30	3	11.8	1.1357	11.9	1.3420	2.7292**
09 II	30	3	12.6	1.2632	8.1	1.3525	2.6121
09 II	30	3	12.6	1.2632	11.6	1.4287	2.6883*
13 II	30	3	12.8	1.1856	6.9	1.1443	2.4816
13 II	30	3	12.8	1.1856	9.2	1.3407	2.6780*
13 II	30	3	12.8	1.1856	10.3	1.3567	2.6940*
14 II	30	2	12.5	1.1761	1.6	0.8636	2.3865
17 II	30	4	12.4	1.2368	4.0	1.3407	2.5019
17 II	30	4	12.4	1.2368	7.1	1.4376	2.4988*
01 III	40	6	11.1	1.0212	7.4	1.3156	2.5163
01 III	40	6	11.1	1.0212	8.0	1.2644	2.4650
01 III	40	6	11.1	1.0212	8.0	1.1774	2.3780
02 III	40	6	12.3	1.1409	5.8	1.4406	2.5215
02 III	40	5	12.7	1.1523	7.5	1.4171	2.5658
03 III	40	2	16.6	1.5478	11.1	1.5055	2.6573*
03 III	40	2	16.6	1.5478	6.0	1.2325	2.3844
10 III	40	4	12.9	1.2007	8.0	1.3737	2.5709
10 III	40	4	12.9	1.2007	8.6	1.3535	2.5507*

Table 6 (cont.)

Date	Salinity (ppt)	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-}$
10 III	40	4	12.9	1.2007	5.7	1.2385	2.4357
14 III	40	4	14.2	1.3734	6.0	1.3891	2.4136
14 III	40	4	14.2	1.3734	10.9	1.6428	2.6674**
24 III	40	2	13.3	1.1903	7.9	1.0939	2.6025
09 VI	10	5	12.6	1.2148	5.8	1.2187	2.3049
09 VI	10	5	12.6	1.2148	10.4	1.3667	2.4529*
09 VI	10	5	12.6	1.2148	6.9	1.2882	2.3744
09 VI	10	5	12.6	1.2148	11.0	1.4459	2.5321*
10 VI	10	2	17.5	1.6258	6.9	1.2699	2.3430
10 VI	10	2	17.5	1.6258	11.8	1.4094	2.4826*
10 VI	10	2	17.5	1.6258	8.3	1.2836	2.3568
10 VI	10	2	17.5	1.6258	12.3	1.3815	2.4536*
12 VI	10	5	12.6	1.2148	6.4	1.2698	2.3560
12 VI	10	5	12.6	1.2148	10.4	1.2976	2.3838*
12 VI	10	5	12.6	1.2148	10.4	1.3599	2.4461*
13 VI	10	2	17.5	1.6258	8.3	1.3076	2.3808
13 VI	10	2	17.5	1.6258	14.2	1.5197	2.5928**
16 VI	20	4	10.7	1.0414	6.3	1.1051	2.4616
16 VI	20	4	10.7	1.0414	8.8	1.1703	2.5269
16 VI	20	4	10.7	1.0414	10.7	1.2714	2.6280*
16 VI	20	4	10.7	1.0414	11.3	1.3140	2.6705*
19 VI	20	2	17.5	1.6128	7.8	1.4699	2.5561
19 VI	20	2	17.5	1.6128	12.7	1.6150	2.7012

Table 6 (cont.)

Date	Salinity (ppt)	No. of Fish	Ave. Total Length (cm)	Log Ave. Wt. (g)	Swimming Speed ($L^{0.5}s^{-1}$)	Log mgO_2h^{-1}	Log $mgO_2kg^{-1}h^{-}$
19 VI	20	2	17.5	1.6128	9.3	1.4653	2.5514
19 VI	20	2	17.5	1.6128	13.7	1.6346	2.7208**
20 VI	20	6	12.1	1.1461	5.9	1.3271	2.4208
20 VI	20	6	12.1	1.1461	8.3	1.4933	2.5690
20 VI	20	6	12.1	1.1461	10.6	1.4837	2.5594
20 VI	20	6	12.1	1.1461	13.0	1.5444	2.6201*
21 VI	20	5	12.4	1.1847	7.0	1.1922	2.3086
21 VI	20	5	12.4	1.1847	14.0	1.4933	2.6096*

to determine means at individual salinity levels, are separately available but will be reproduced only in the figures that follow below.

Multiple Regressions

The multiple regressions that relate the expected log oxygen consumption rate $\hat{Y}$ in mgO_2h^{-1} to log weight, swimming rate, and linear and quadratic salinity terms and the regressions that relate the log oxygen consumption rate per unit weight $\hat{Y}_{kg}$ in $mgO_2kg^{-1}h^{-1}$ to swimming rate and salinity are in Table 7 for all three species. Table 7 contains also the regressions after elimination of data for groups with highly variable lengths ("edited" equations).

The statistical significance of each of these equations ($P<<0.001$) indicates about average variability for experiments of this type. The Atlantic croakers were the most variable, judging from the standard error of estimates and the multiple correlations in Table 7. Although not tabulated separately, the statistical properties of the separate partial regression coefficients are of some interest. Briefly all the b_w and b_v have a probability of chance occurrence of $P<<0.001$; the b_s and b_{ss} have some rather interesting statistical properties, however. The salinity coefficients nearly all occur with highly significant probabilities ($P<0.01$) for the spotted seatrout and the Atlantic croakers in Eq. 4 and 4 Ed. For Atlantic croakers in Eq. 3 and 3 Ed. and for all the red drum, the b_s and b_{ss} were statistically nonsignificant ($P>0.05$).

Table 7. Oxygen consumption regressions over 10,20,30,40 ppt salinities and 15°C for three fish species; activity range from resting to maximum sustained swimming rate. Alternate equations "edited" (Ed.) for excessive size variability of groups.

Eq. No.	N	Expected log O_2 Uptake Rate $\hat{Y}$ or $\hat{Y}_{kg}$		Constant a	Log Wt. (g) b_wX_w	Activity $L^{\frac{1}{2}}s^{-1}$ b_vX_v	Salinity (ppt) Linear b_sX_s	Salinity (ppt) Quadratic $b_{ss}X_s^2$	Standard Error of Estimate σ	Multiple Correlation R
Redfish:										
1	101	$\hat{Y}_{kg}$	=	2.1115 +		+ 0.0410X_v	+ 0.0007X_s	+0.00006X_s^2	0.0739	0.94
1 Ed.	86	$\hat{Y}_{kg}$	=	2.1323 +		- 0.0407X_v	- 0.0024X_s	+0.00013X_s^2	0.0693	0.95
2	101	$\hat{Y}$	=	-0.7793 +	0.9903X_w	+ 0.0393X_v	- 0.0053X_s	+0.00016X_s^2	0.1218	0.97
2 Ed.	86	$\hat{Y}$	=	-0.7806 +	1.0211X_w	+ 0.0383X_v	- 0.0101X_s	+0.00025X_s^2	0.1260	0.97
Atlantic croaker:										
3	60	$\hat{Y}_{kg}$	=	2.2729 +		+ 0.0283X_v	- 0.0119X_s	+0.00027X_s^2	0.1546	0.69
3 Ed.	48	$\hat{Y}_{kg}$	=	2.2733 +		+ 0.0293X_v	- 0.0134X_s	+0.00032X_s^2	0.1578	0.73
4	60	$\hat{Y}$	=	0.1522 +	0.6459X_w	+ 0.0331X_v	- 0.0324X_s	+0.00066X_s^2	0.1771	0.86
4 Ed.	48	$\hat{Y}$	=	0.2646 +	0.6484X_w	+ 0.0309X_v	- 0.0449X_s	+0.00092X_s^2	0.1843	0.87
Spotted seatrout:										
5	80	$\hat{Y}_{kg}$	=	1.9472 +		+ 0.0374X_v	+ 0.0184X_s	-0.00027X_s^2	0.0637	0.94
5 Ed.	54	$\hat{Y}_{kg}$	=	1.9495 +		+ 0.0393X_v	+ 0.0155X_s	-0.00021X_s^2	0.0605	0.96
6	80	$\hat{Y}$	=	1.0729 +	0.9963X_w	+ 0.0376X_v	+ 0.0190X_s	-0.00028X_s^2	0.0650	0.99
6 Ed.	54	$\hat{Y}$	=	-1.0239 +	0.9867X_w	+ 0.0396X_v	+ 0.0152X_s	-0.00021X_s^2	0.0611	0.99

Scope for Activity

Red drum. From the data in Tables 1 and 3 for each salinity, averages of metabolic rates at maximum sustained swimming rates and averages at resting rates are plotted in Fig. 1. Also in Fig. 1 for each salinity the individual maximum active and minimum resting metabolic rates are plotted. The scopes -- differences between maximum and standard estimates -- are plotted in Fig. 2 both for differences between averages and for differences between maximum and minimum metabolic rates. Calculated metabolic rates at overall average weights, at each salinity level, and at average maximum or at zero swimming rates from Equation 1, Table 7 are in Fig. 3; the corresponding scope plots are in Fig. 4. Because quite similar values resulted from utilization of Equations 1 Ed., 2, and 2 Ed. these equations were not used.

Red drum "adjusted" scope values. At each of the salinity intervals log weight (g) on log length (TL) regressions were calculated from data in Tables 1 and 4. The regression slopes, as a measure of condition, were: 3.109, 2.628, 3.092 and 3.057 at respective salinities of 10, 20, 30 and 40 ppt. Only at 20 ppt was the coefficient rather low compared to the others and to the 3.04 value from Harrington, et al. (1978) for this species. Accordingly, an upward "adjustment" in scope for the 20 ppt data would approximate 3.04/2.628 = 1.2. This procedure was suggested by the earlier work on spotted seatrout for which one group of fish at 30 ppt were very much more slender than the groups at other salinities and for which the active metabolism

Fig. 1. Juvenile red drum metabolism and salinity relationships at 15°C. Circles indicate averages of observed values at maximum activity and resting metabolic rates at each salinity level. Triangles indicate individual maximum and minimum metabolic rates observed at each salinity.

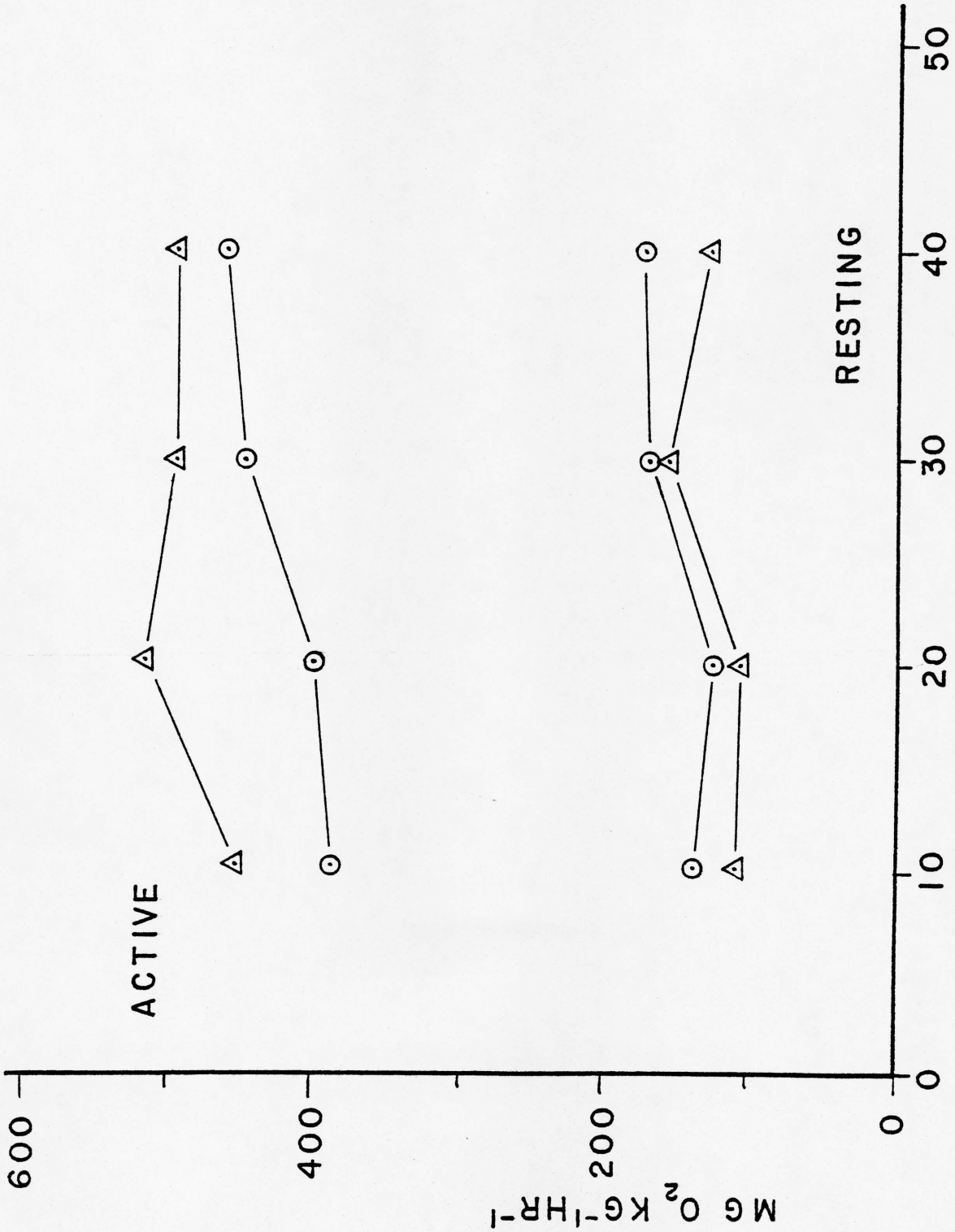

ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
600
400
200
0
0
10
20
30
40
50
SALINITY — PPT

Figure 1.

Fig. 2. Juvenile red drum scope for activity and salinity relationships at 15°C. Circles denote scope values based on average rates (Fig. 1); triangles denote scope values based on extreme rates.

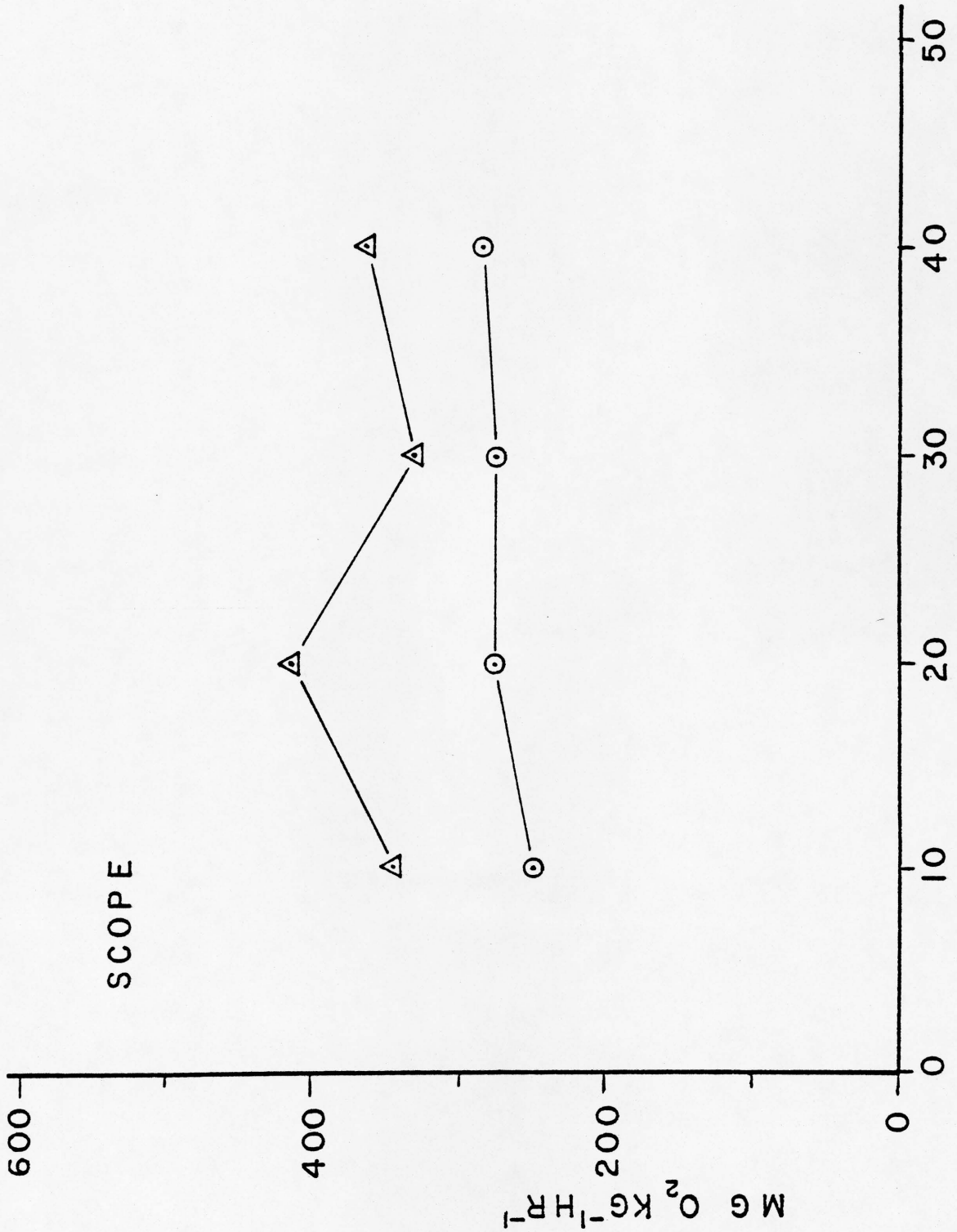


Figure 2.

Fig. 3. Juvenile red drum metabolic and salinity relationships at 15°C as calculated for average maximum and zero activities and for average weights.

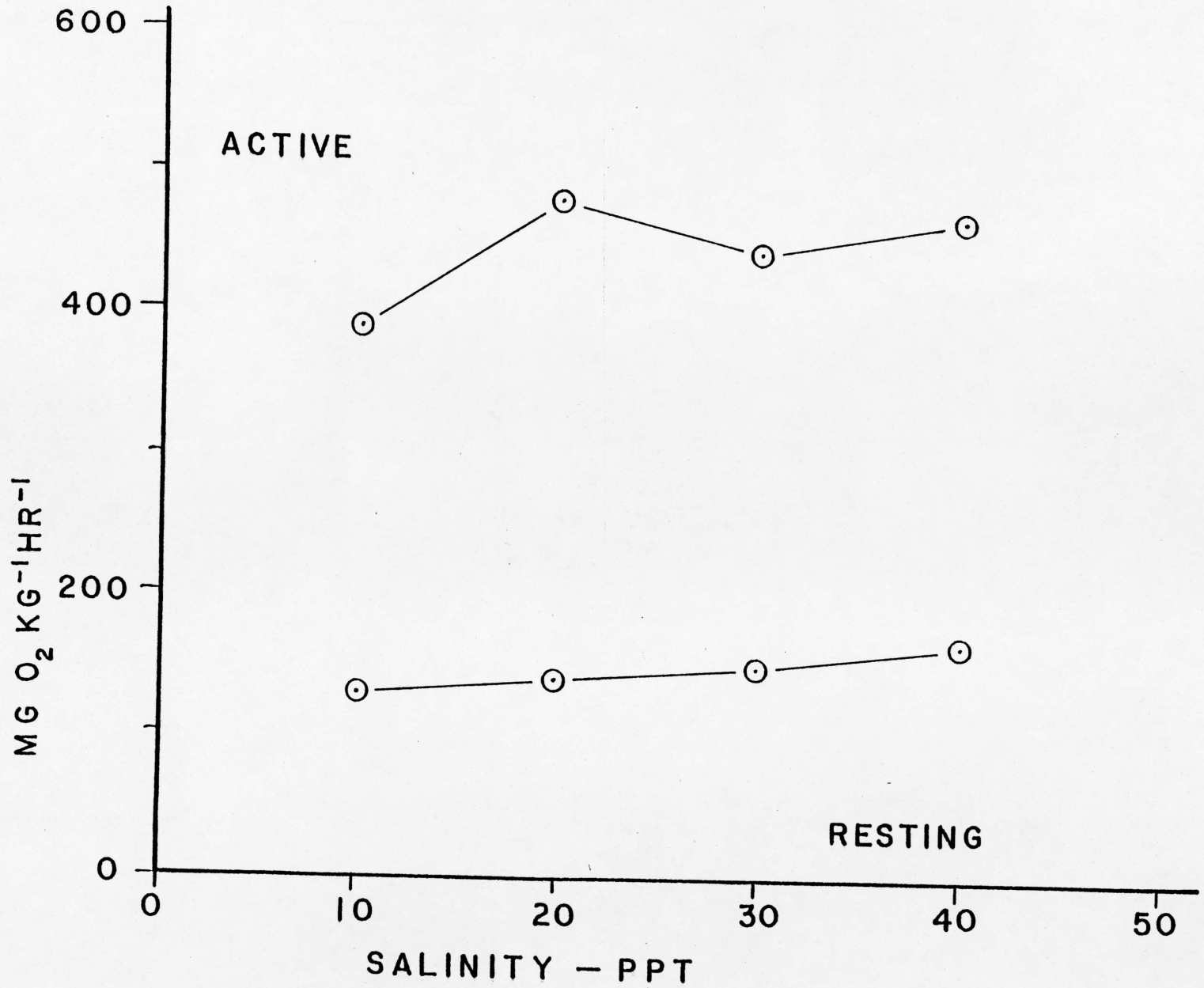

600
400
200
0
ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
0
10
20
30
40
50
SALINITY — PPT

Figure 3.

Fig. 4. Juvenile red drum scope for activity at 15°C and selected salinity levels as based on calculated active and resting metabolic rates. See Table 7 and text.

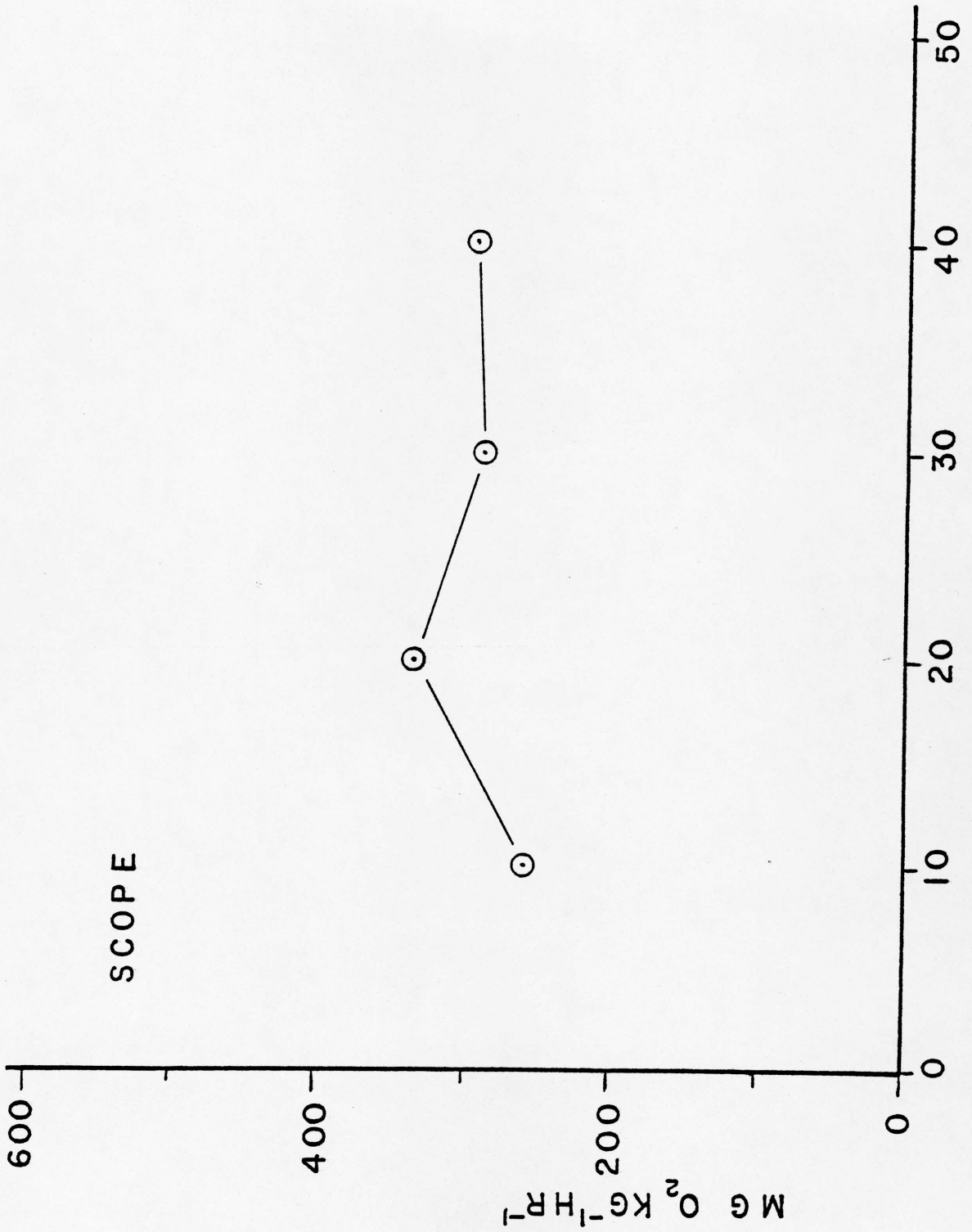


Figure 4.

was proportionately reduced (see Wohlschlag and Wakeman 1978). By raising the scope value by 1.2, the scope relationships appear as in Fig. 5.

Atlantic croaker. From the data in Tables 2 and 5 for each salinity, averages of metabolic rates at maximum sustained swimming rates and averages at resting rates are plotted in Fig. 6. Fig. 7 has the appropriate scope data plotted for the averages and extreme values at each salinity. Calculated metabolic rates from Eq. 3, Table 7 at overall average weights, at each salinity level, and at average maximum or zero swimming rates are plotted in Fig. 8 with the corresponding scope plots in Fig. 9. The other equations, 3 Ed., 4, and 4 Ed., yielded similar values and were not used separately.

Atlantic croaker "adjusted" scope values. From the data in Tables 2 and 5 and at each salinity, log weight on log length regressions for determination of the slopes can be used as a measure of condition to compare with 3.1 (Parker 1971), 3.15 (Dawson 1965) and 3.15 (Avault, et al. 1969). The slopes (regression coefficients) were 2.8, 2.9, 3.6 and 3.1 for 10, 20, 30 and 40 ppt, respectively. By comparing the average calculated scopes from Eq. 3 to the "hypothetical" value of 3.1 from the other studies, the comparative adjusted values result as shown in Fig. 10.

Spotted seatrout. From Tables 3 and 6 are calculated the averages for metabolic rates at active and resting rates and for maximum sustained swimming velocities pertinent for each salinity level. The averages and the extreme upper and lower values are plotted in Fig. 11. The corresponding scope calculations are in

Fig. 5. Juvenile red drum "adjusted" scope values for condition at 15°C and selected salinity levels. See text and Fig. 4.

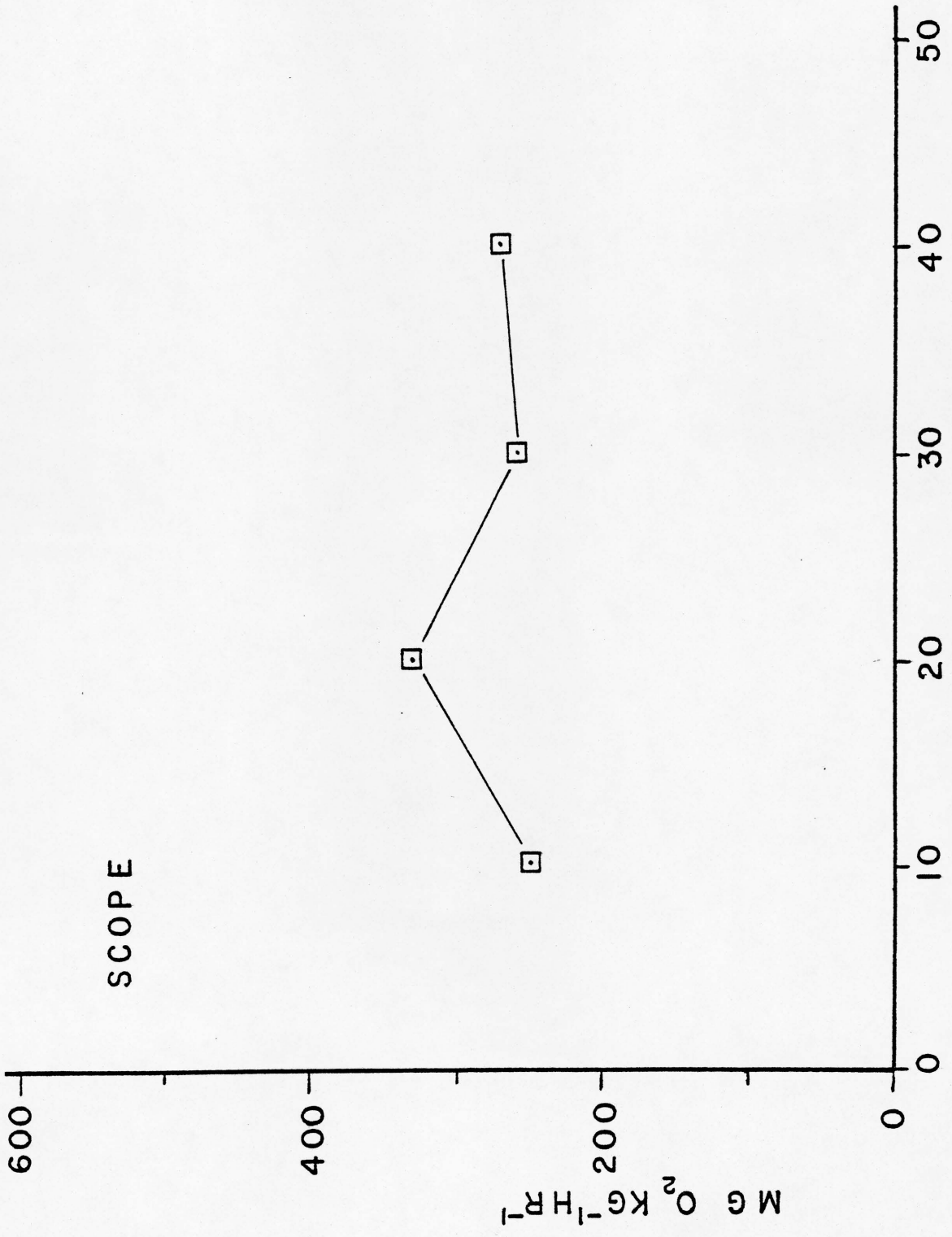


Figure 5.

Fig. 6. Juvenile Atlantic croaker metabolism and salinity relationships at 15°C. Circles denote averages of observed values at maximum activity and resting rates (zero activity) at each salinity level. Triangles denote individual maximum and minimum metabolic rates observed at each salinity.

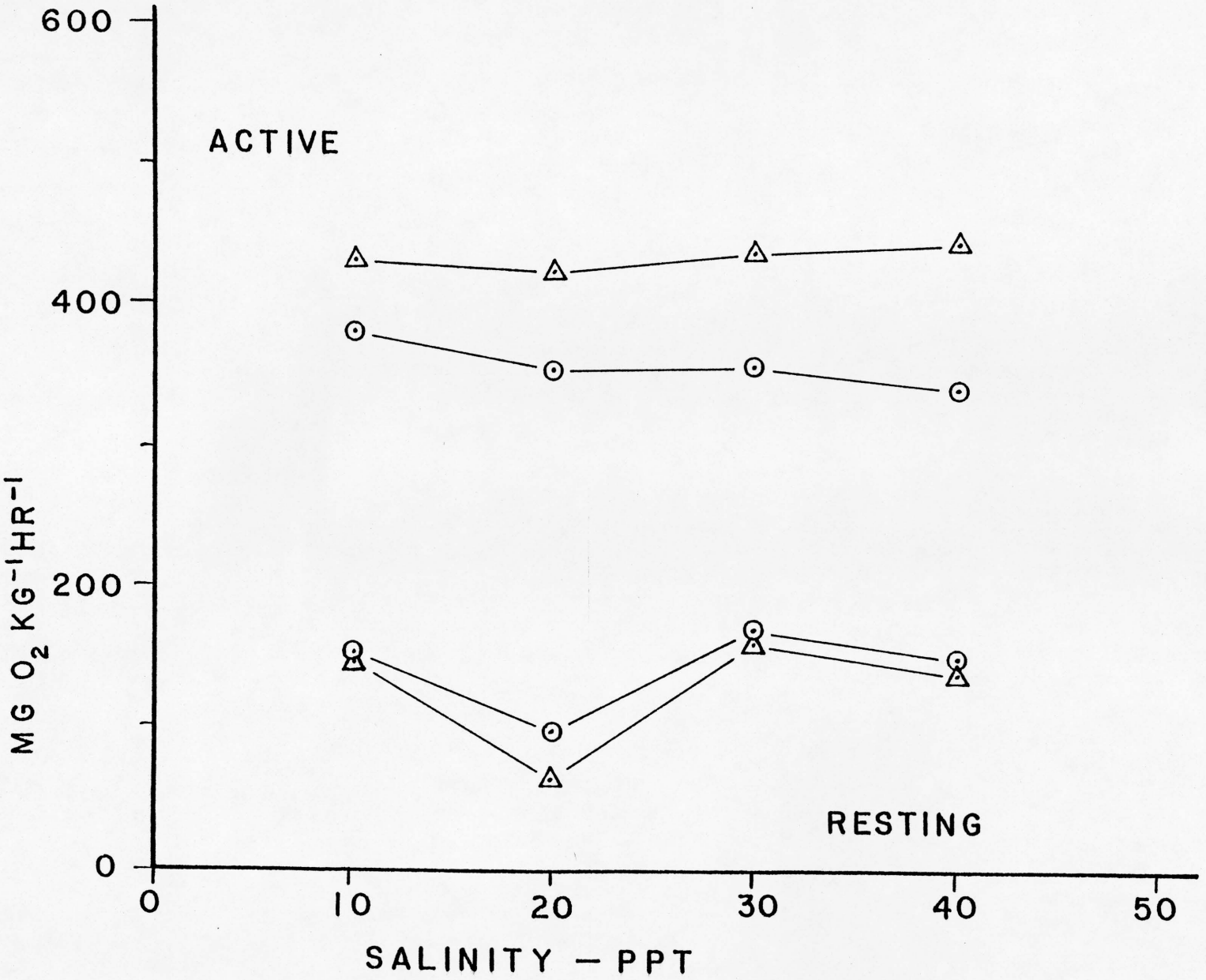

600
400
200
0
ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
0
10
20
30
40
50
SALINITY — PPT

Figure 6.

Fig. 7. Juvenile Atlantic croaker scope for activity and salinity relationships at 15°C. Circles denote scope values based on average rates (Fig. 1); triangles denote scope values based on extreme rates.

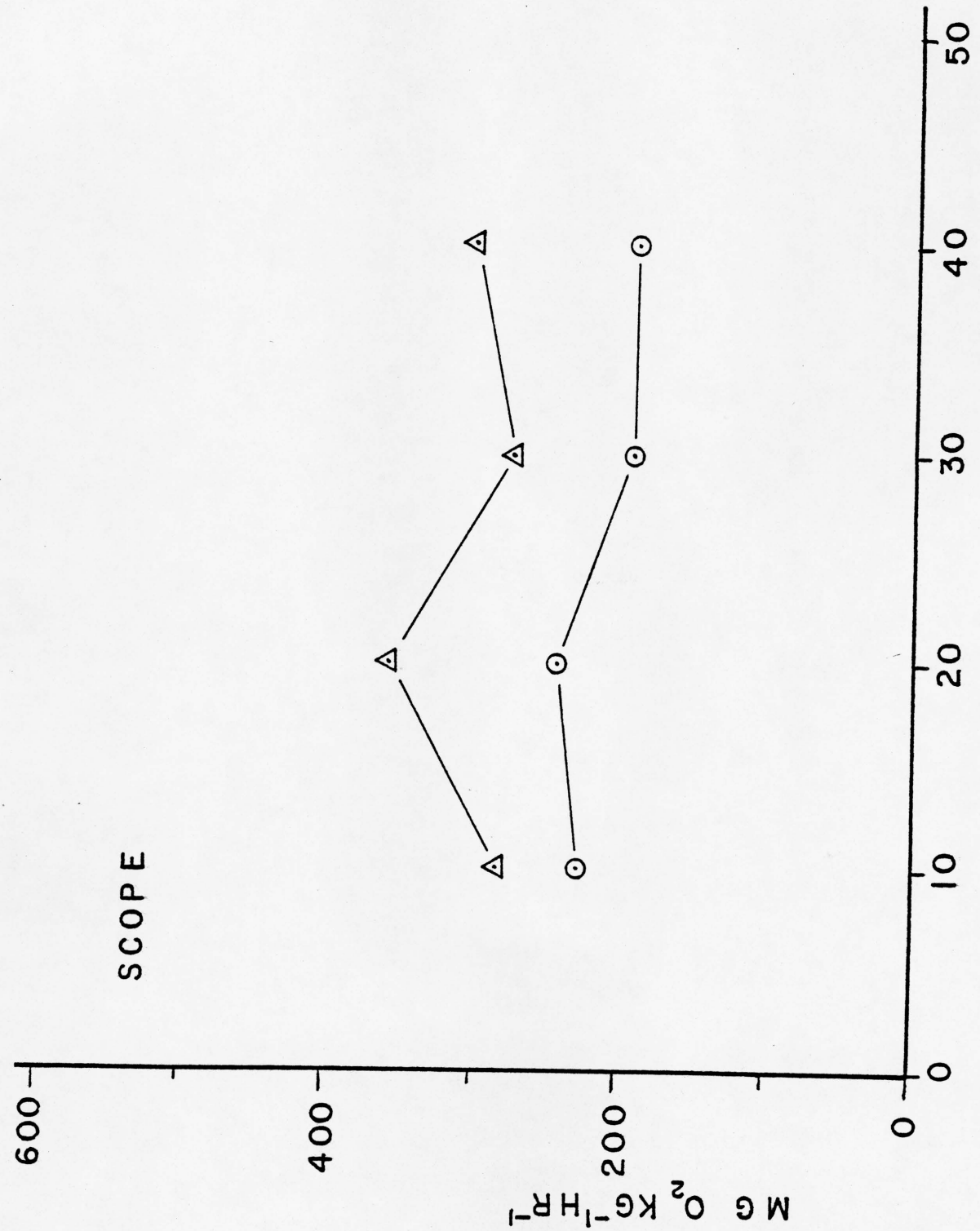


Figure 7.

Fig. 8. Juvenile Atlantic croaker metabolic and salinity relationships at 15°C as calculated for average maximum and zero activities and for average weights.

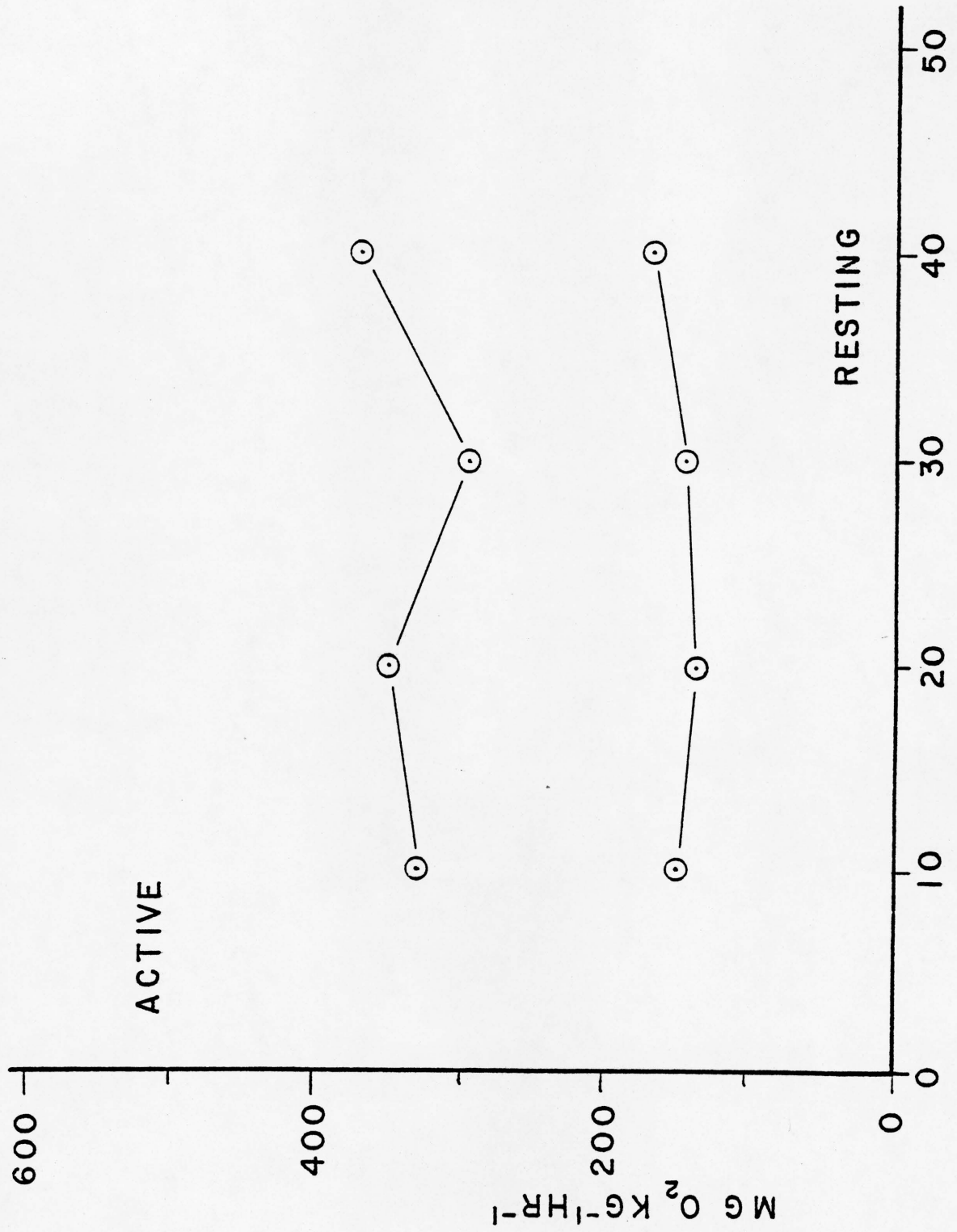

ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
600
400
200
0
0
10
20
30
40
50
SALINITY — PPT

Figure 8.

Fig. 9. Juvenile Atlantic croaker scope for activity at 15°C and selected salinity levels as based on calculated active and resting metabolic rates. See Table 7 and text.

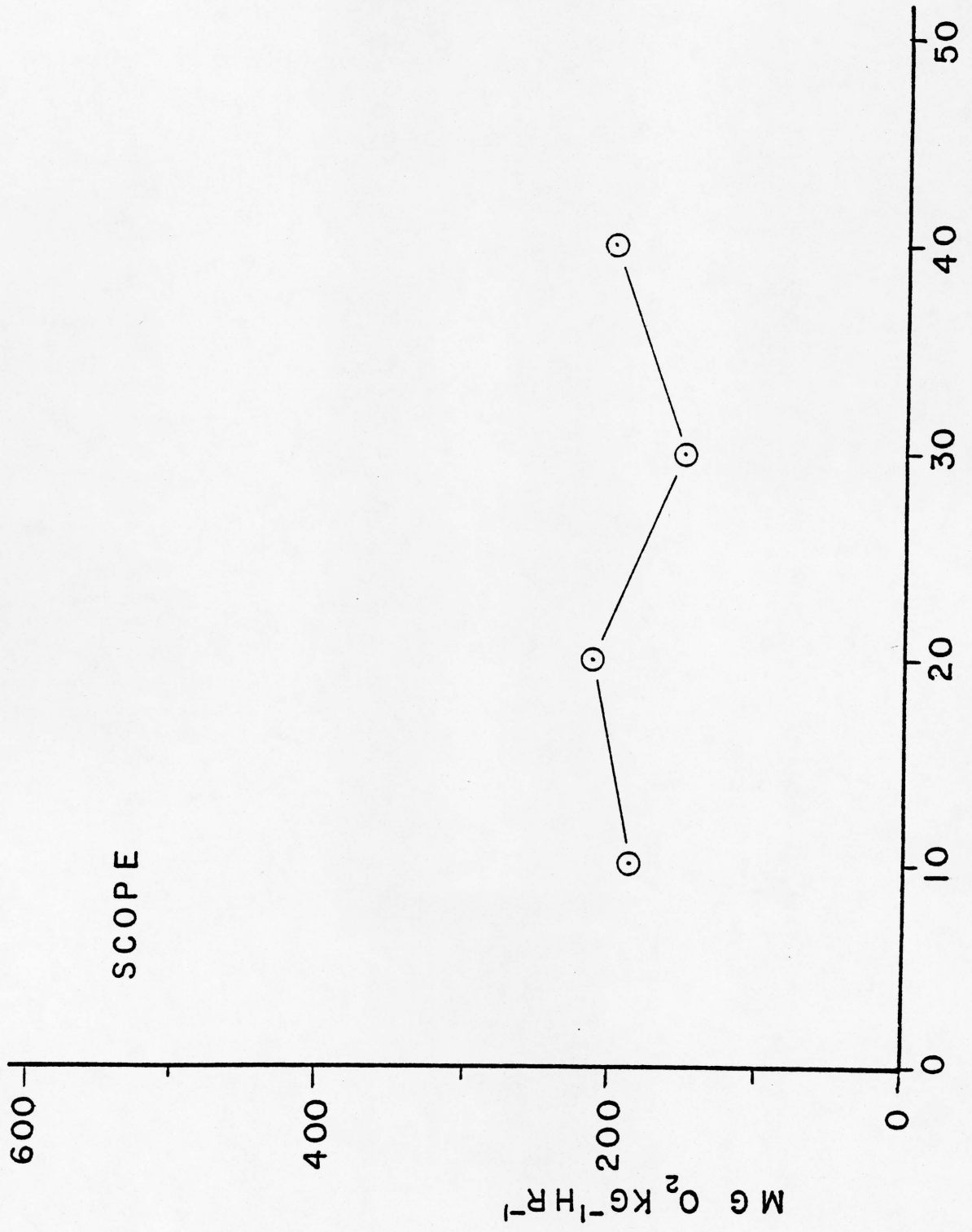


Figure 9.

Fig. 10. Juvenile Atlantic croaker scope values "adjusted" for condition at 15°C and selected salinity levels. See text and Fig. 9.

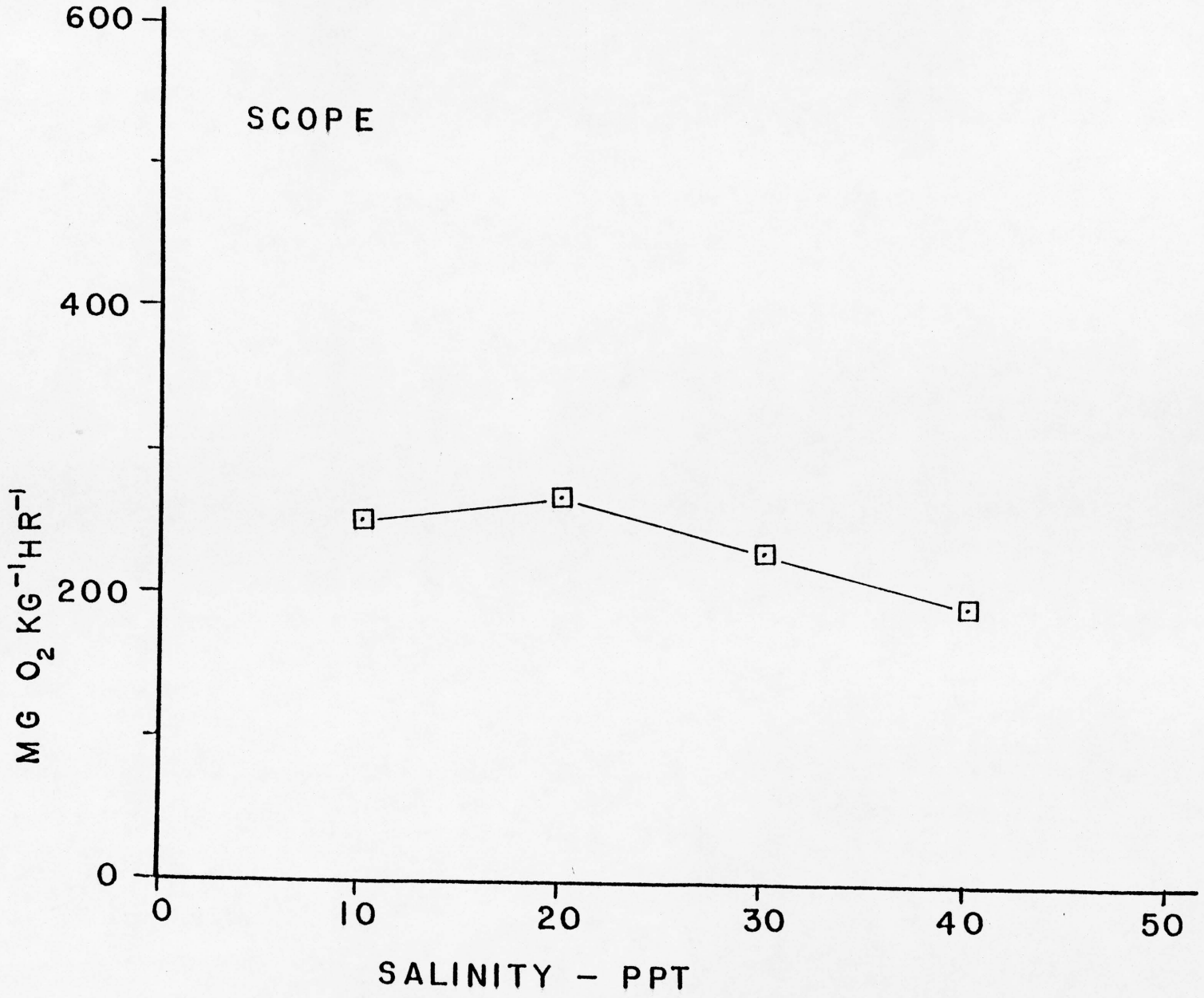


Figure 10.

Fig. 11. Juvenile spotted seatrout metabolism and salinity relationships at 15°C. Circles denote averages of observed metabolic values at maximum activity and at resting levels for each salinity. Triangles denote individual observed maximum and minimum metabolic rates for each salinity.

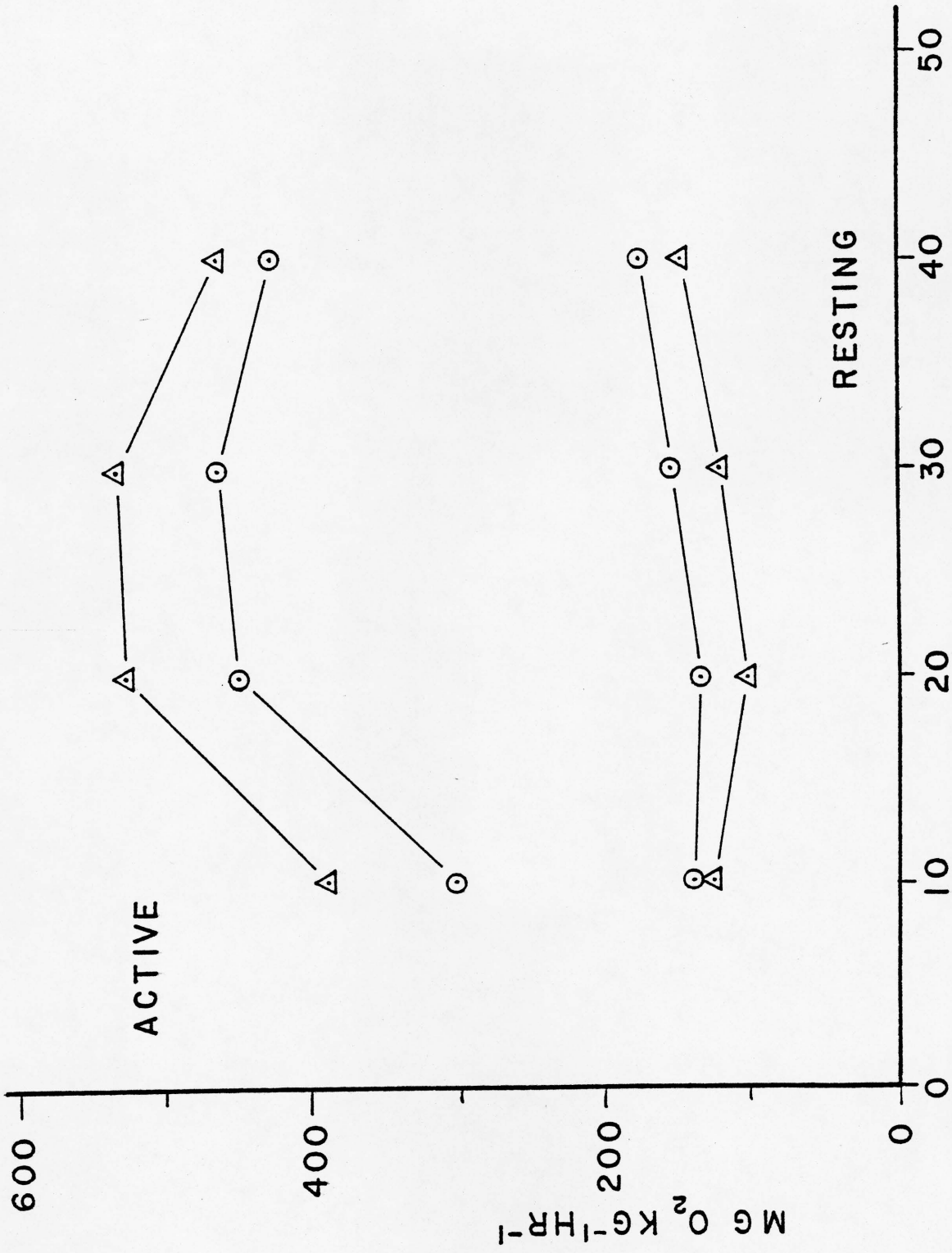

ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
SALINITY — PPT
600
400
200
0
0
10
20
30
40
50

Figure 11.

Fig. 12. Calculated metabolic rates from Eq. 5, Table 7 at average weights, at each salinity level and at average maximum and zero swimming rates are plotted in Fig. 13 with corresponding scope values plotted in Fig. 14. Equations 5 Ed., 6 and 6 Ed. were not used; they yielded results similar to those from Eq. 5.

Spotted seatrout "adjusted" scope values. By utilizing data from Tables 3 and 6 for each salinity interval log weight on log length regressions were prepared to compare, as a measure of condition, with the slope of 3.06 from Harrington, et al.(1978). The regression slopes were, respectively, 2.88, 2.73, 2.36 and 2.95 for the 10, 20, 30 and 40 ppt salinity intervals. By "adjusting" the scope values in Fig. 14 according to these regressions and the Harrington value of 3.06, the respective ratios were 1.0, 1.1, 1.28 and 1.0, the scopes now become those plotted in Fig. 15.

Adult-Juvenile Scope Comparisons

Red drum. From Table 3 of the 1977 report the only observations that served as a reference for the adult fish extrapolations to 15°C were at 20 ppt and 15°C. The maximum adult sustained swimming velocities ($L^{1/2}s^{-1}$) at 28°C (at plotted in Fig. 10 of the 1977 report) would be reduced from 17.98 to 15.13 at 10 ppt, from 21.65 to 17.49 at 20 ppt, from 22.21 to 14.52 at 30 ppt and from 17.77 to 13.91 at 40 ppt. From the active oxygen consumption rates per kilogram at 28°C in Fig. 5 were subtracted appropriate amounts for reductions in swimming velocity and 13°C temperature from 28° to 15°C as determined by

Fig. 12. Juvenile spotted seatrout scope for activity and salinity relationships at 15°C. Circles indicate scope values based on average rates (Fig. 5); triangles indicate scope values based on extreme rates.

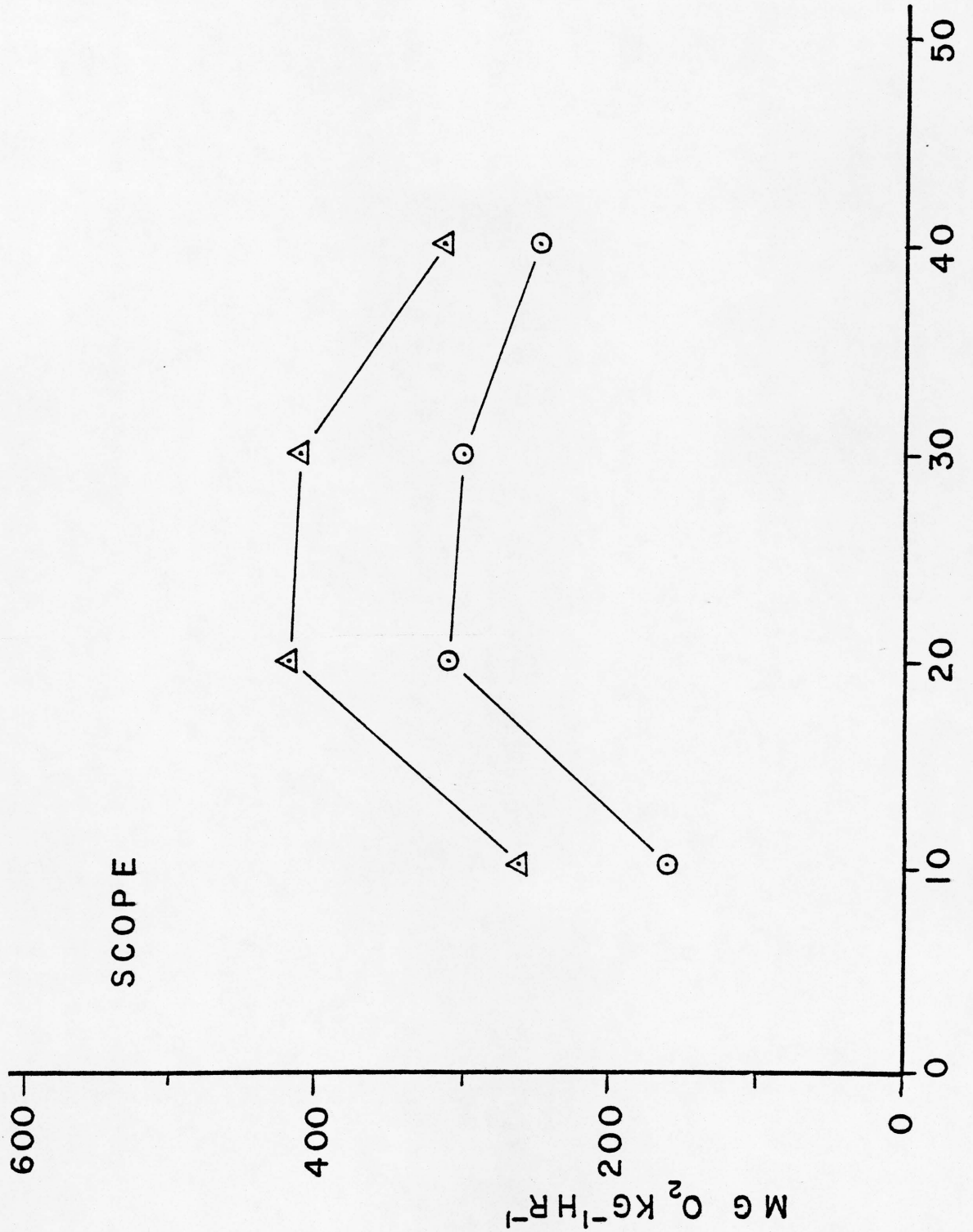


Figure 12.

Fig. 13. Juvenile spotted seatrout metabolic and salinity relationships at 15°C as calculated for average maximum and zero activities and for average weights.

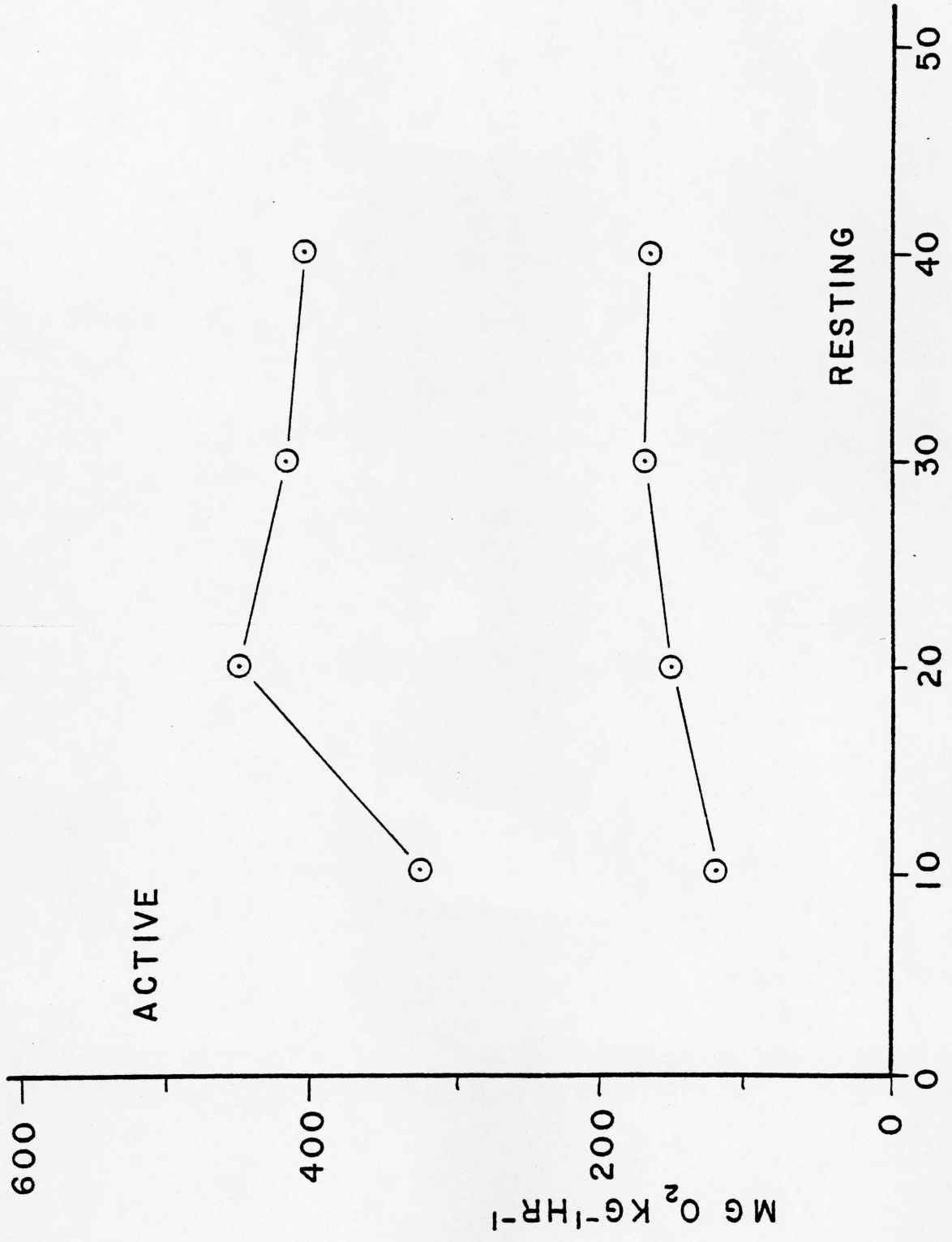

ACTIVE
RESTING
MG O_2 $KG^{-1}HR^{-1}$
600
400
200
0
0
10
20
30
40
50
SALINITY — PPT

Figure 13.

Fig. 14. Juvenile spotted seatrout scope for activity at 15°C and selected salinity levels as based on calculated active and resting metabolic rates. See Table 7 and text.

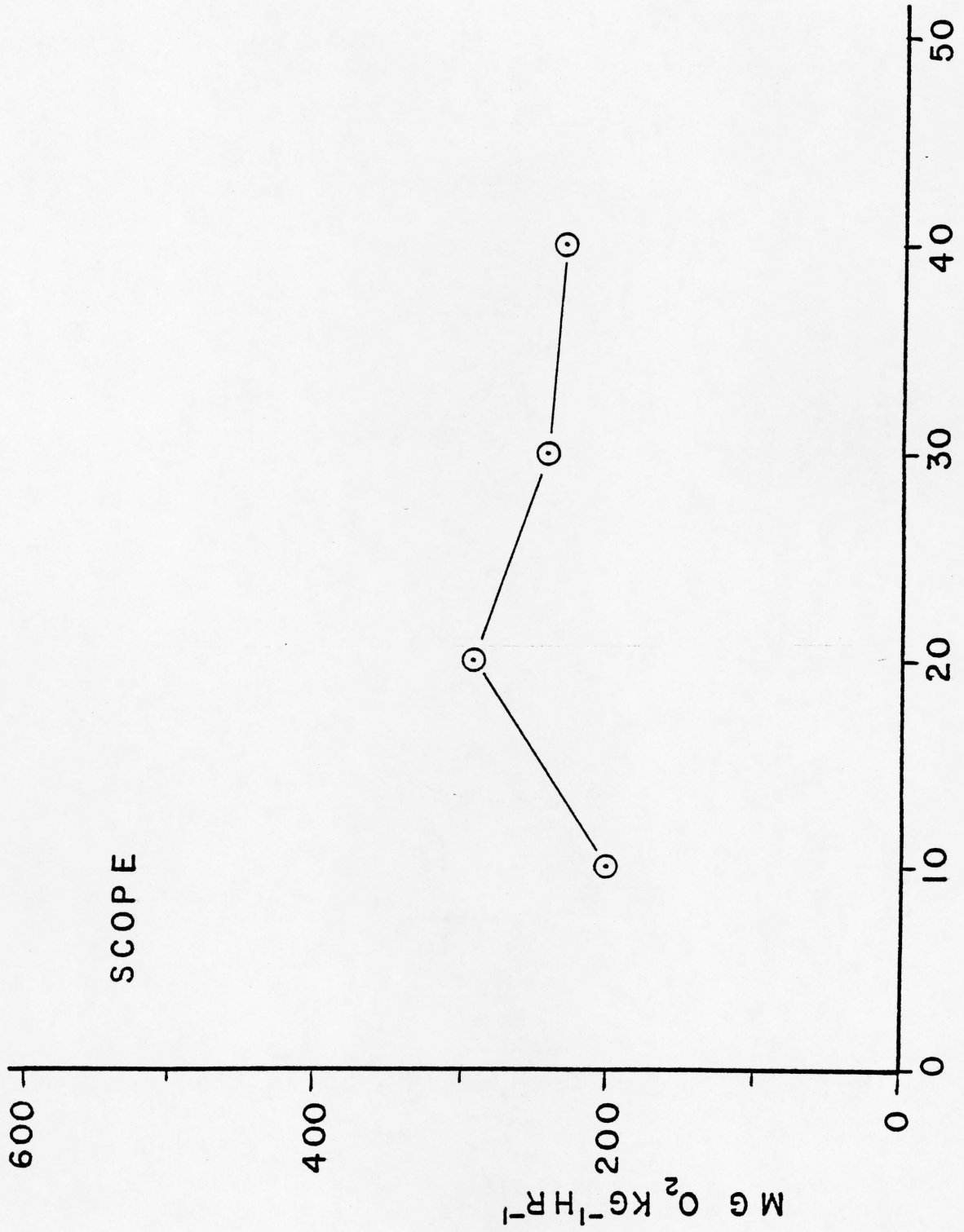


Figure 14.

Fig. 15. Juvenile spotted seatrout scope values "adjusted" for condition at 15°C and selected salinity levels. See text and Fig. 14.

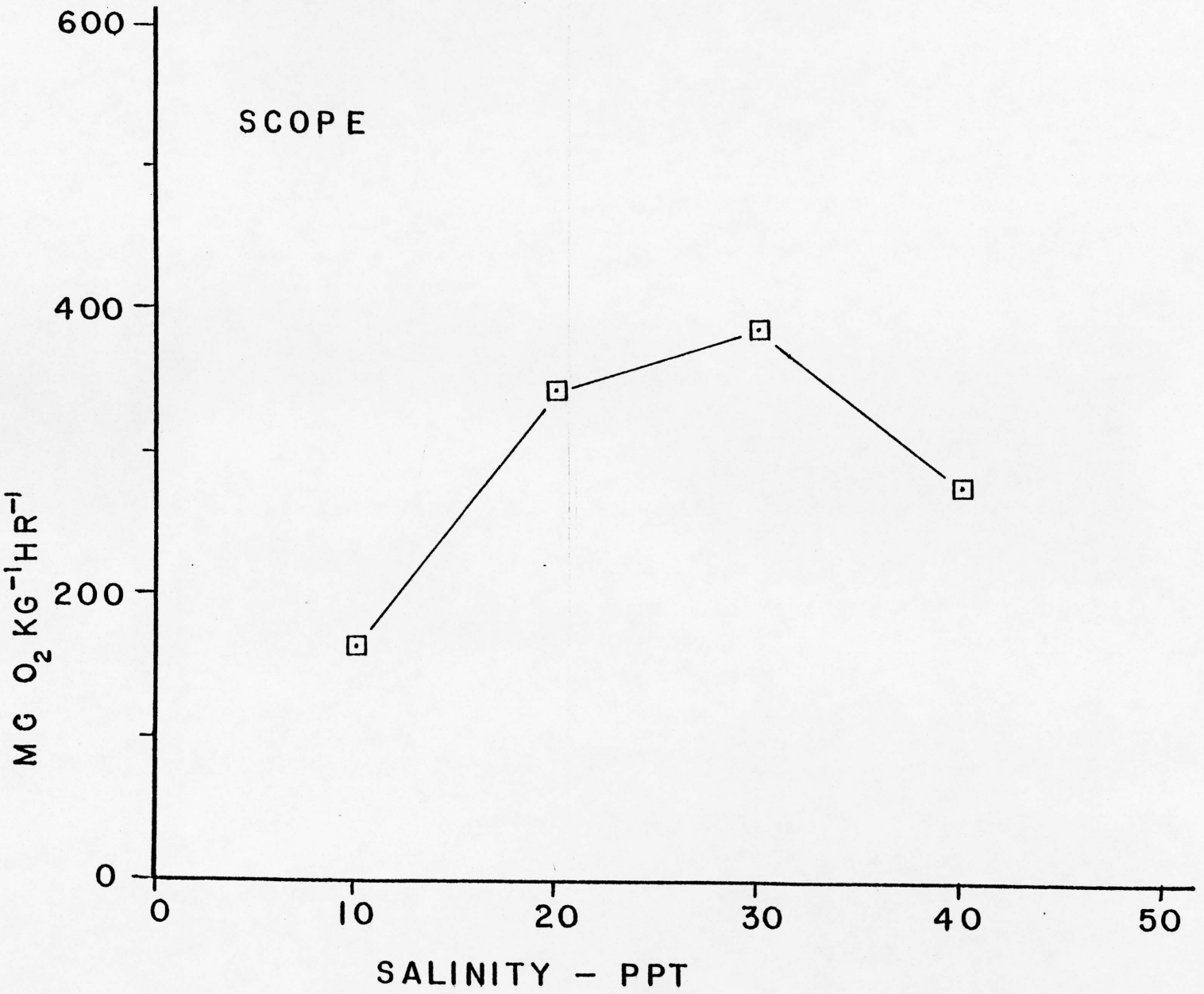


Figure 14.

Eq. 3B of the 1977 report:

$$\hat{Y}_{kg} = 1.8965 + 0.0119X_t + 0.0325X_v - 0.0102X_s + 0.001X_s^2.$$

For example, the $\hat{Y}_{kg}$ observed at 28° and 10 ppt (Fig. 5) of 586.1 ($\log_{10}$ = 2.76797) $mgO_2kg^{-1}h^{-1}$ would be reduced by (28°-15°)(0.0119) = 0.15535 log units for temperature and (17.98-15.13)(0.0325) = 0.0926 log units for swimming velocity to $\hat{Y}_{kg}$ = 2.5200 or 331.1 $mgO_2kg^{-1}h^{-1}$ at 15° and 10 ppt. Similarly, the standard rate was reduced only for temperature (0.15535 log units). Alternatively, the scope value at 28° could be reduced for both temperature and diminished swimming activity at 15°C. The comparative scope values for the juveniles and adults are in Fig. 16.

Atlantic croaker. Attempts to extrapolate 1977 report data to 15° were variously useful. Attempts to determine how much swimming velocity changed in $L^{1/2}s^{-1}$ units per degree centigrade were rather unsatisfactory, but the 1977 data for 22° and 18° at 10 ppt yielded a reasonable estimate of 0.42554 $L^{1/2}s^{-1}$ units per degree. This estimate was then applied to the average data used to construct Figures 6 and 11 in the 1977 report, viz.; at an average temperature of 17.3°C and average weight of 145.5 g, N = 138; the swimming velocities were adjusted downward from X_v of 16.0, 17.2, 18.3, and 14.7 $L^{1/2}s^{-1}$ at respective salinities of 10, 20, 30 and 40. The velocity reduction was based on the b_v coefficient of 0.0342 log units in Equation 4B of the 1977 report (p. 68) while the temperature reduction to 15° was based on the b_t coefficient of 0.0234 log units in the same equation.

Fig. 16. Comparison of scope for activity values for juvenile and adult red drum at 15°C. (See text.)

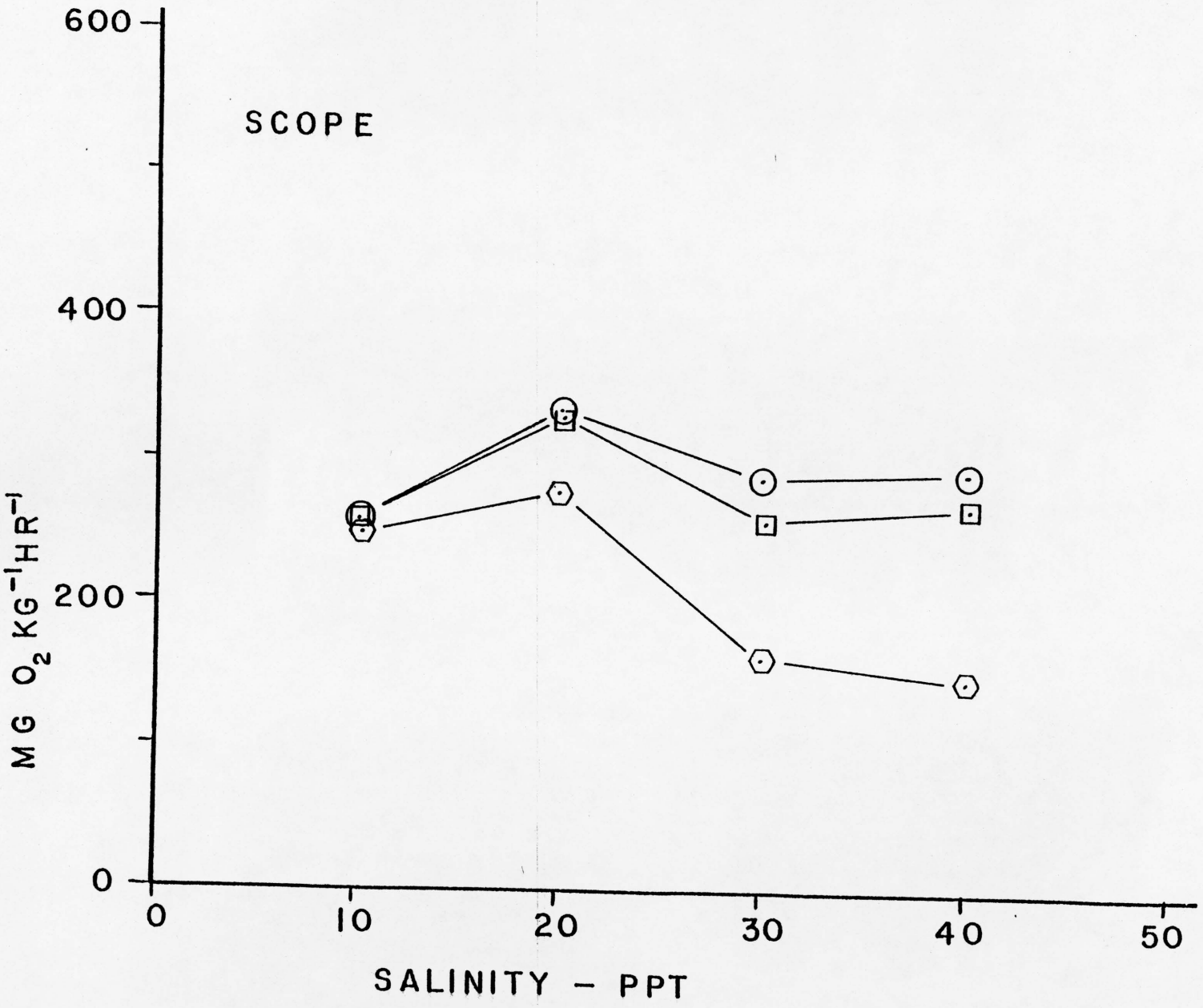


Figure 16.

The data for 15° scope extrapolations for adults, as compared to the maximum and calculated scope determinations from this study are plotted in Fig. 17.

Fig. 17. Comparison of scope for activity values for juvenile and adult Atlantic croaker at 15°C. (See text.)

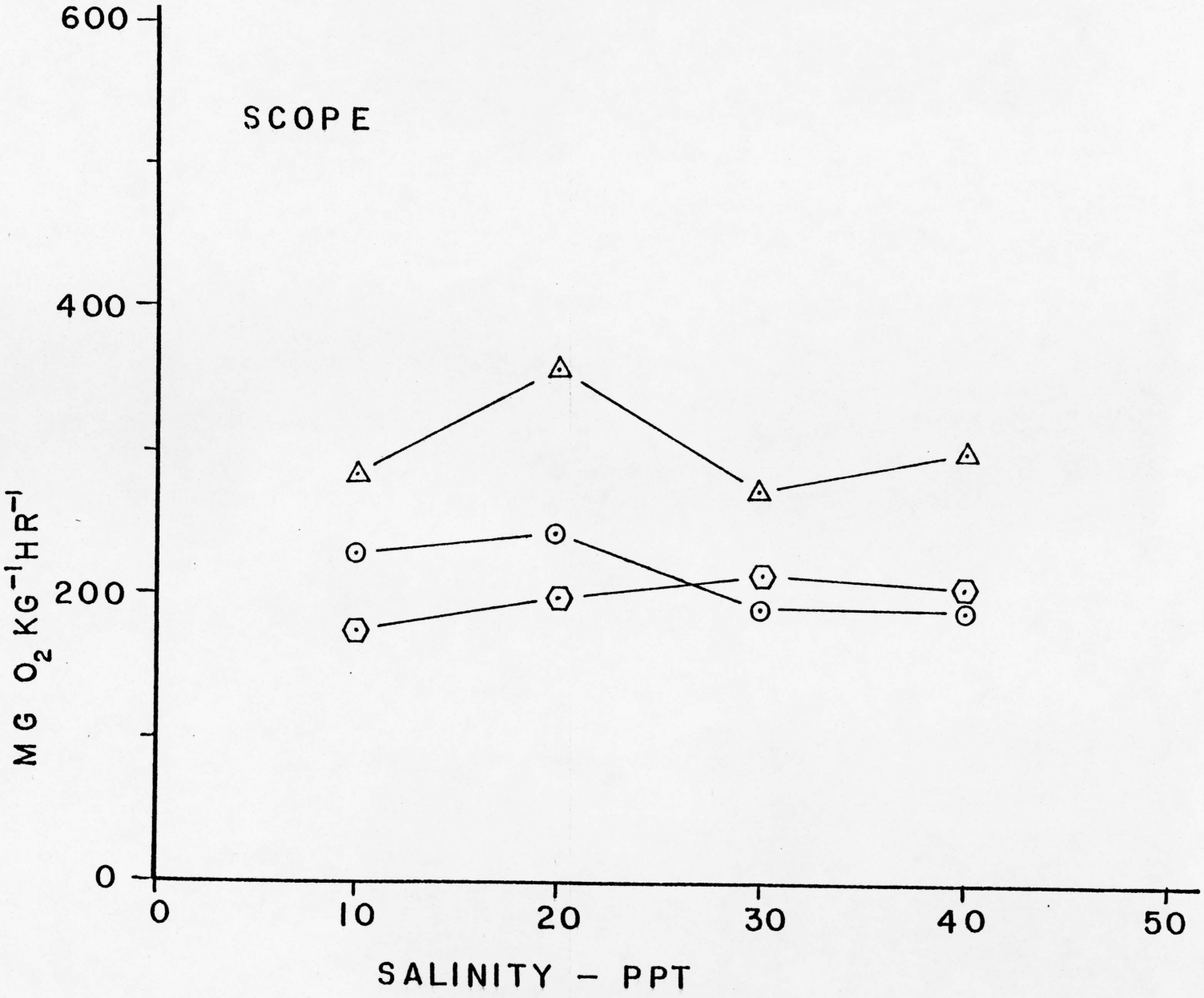
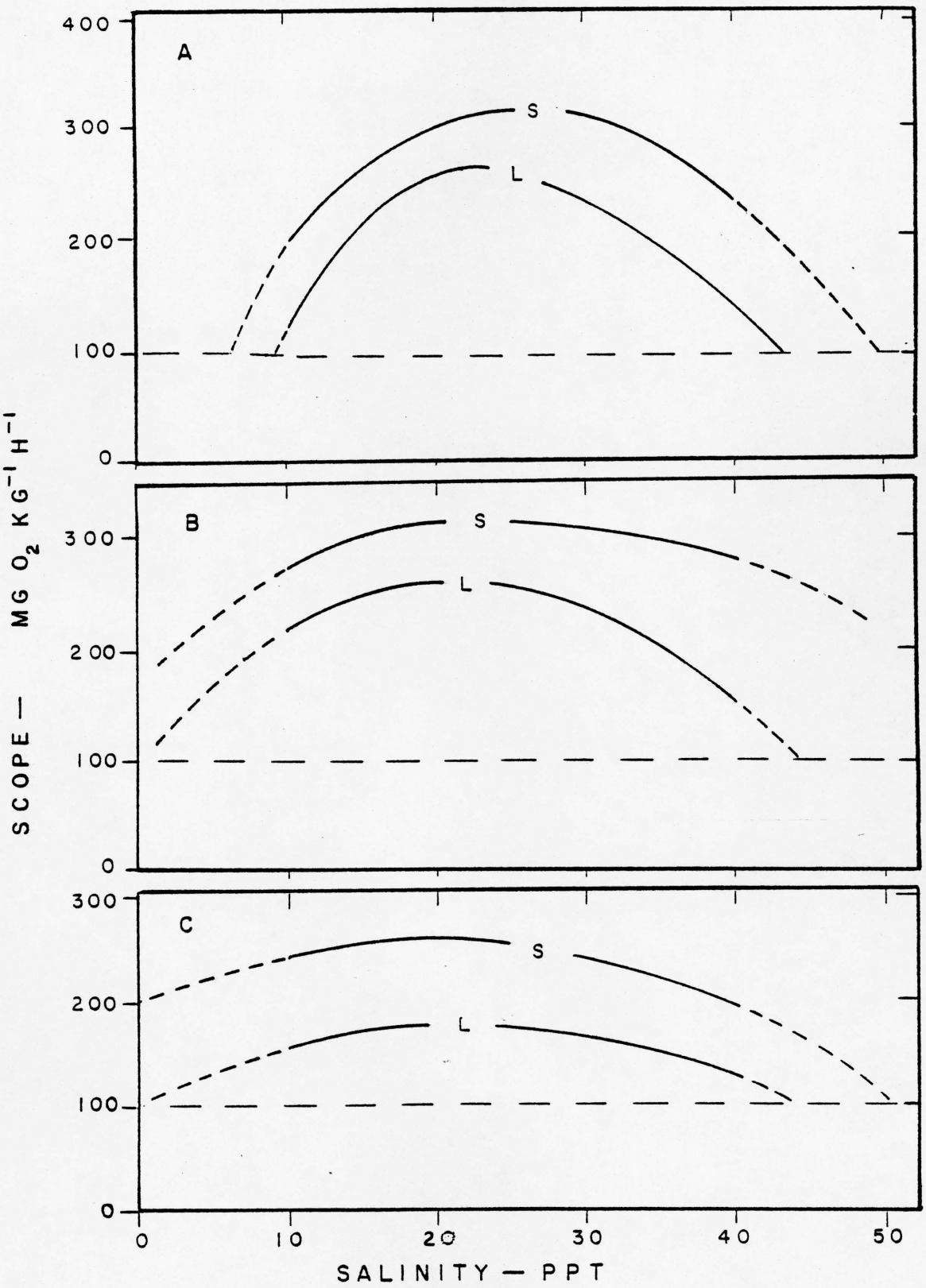


Figure 17.

Spotted seatrout. Since the various previous TDWR studies on active metabolism had been carried out chiefly at 28°C, there were little other data on adults in the previous reports that were directly useful for the 15°C comparisons with juveniles in Figs. 14 and 15 of this study. Without any adjustments for changes in swimming velocity and scope for temperature, the 28°C adult fish data of Wohlschlag and Wakeman (Fig. 1, 1978) can be reduced for temperature alone to 15°C for comparison with Figs. 14 and 15 juvenile data. The reduction was effected by using multiple regression data from the 1976 study (Table 7a, p. 32; Fig. 2, p. 34). The b_t for the lower temperature of about 0.02 was increased to 0.03 to allow for decreased swimming velocities and the 28°C Fig. 1 data of Wohlschlag and Wakeman (1978) reduced directly to 15°. The calculated rates agreed well with the observed rates at 15°C in the 1976 study, allowing for differences in swimming velocities. The adult-juvenile comparisons of the spotted trout are in Fig. 18 and will be considered also in the discussion section below.

Fig. 18. Composite 15°C metabolic scope-salinity curves for large (L) subadult to adult and small (S) juvenile (A) spotted seatrout, (B) red drum and (C) Atlantic croaker. See text for explanation.


A
B
C
S
L
400
300
200
100
0
0
10
20
30
40
50
SCOPE — MG O_2 KG^{-1} H^{-1}
SALINITY — PPT

DISCUSSION

Size of Fish and Seasonal Aspects

A number of experimental and environmental considerations involve the sizes of individuals and schools. The major technical considerations include seasonal field sampling problems and fish of sufficient size and numbers to consume appreciable amounts of oxygen during swimming periods in the 207-liter Blazka chamber.

Acquisition of small sizes for a species that grows rapidly and/or has a brief period for hatching becomes difficult at least during part of the year. For example, small (fingerling) red drum are readily available locally only from March through June; before March, the smaller red drum are difficult to separate from the Atlantic croaker and the spot; after June they tend to be larger than 20 cm and beyond sizes of interest in this study. Juvenile sizes of the slower growing Atlantic croaker and the spotted seatrout generally can be found locally throughout the year.

Local aggregations are often seasonally temperature related. When water temperatures fall much below 20°C, these species tend to be found in deeper waters. Then they are accessible by trawling, which is fairly successful for species like the Atlantic croaker but very damaging to the fine scales of the small spotted seatrout. In addition to deaths from trawling times as short as 5 minutes, trout were also reluctant to begin a laboratory feeding regime and thus were susceptible to additional mortality or debilitation.

In general, making uniform comparisons among several species, all within a restricted size range, is probably not ecologically possible unless each species has approximately equivalent spawning/hatching times and growth rates. Holding laboratory fish under controlled hatching and growing conditions would be physiologically possible and useful, but whether the normal seasonal sequence of growth and metabolic responses would be ecologically pertinent would be difficult to determine. For the small fish used in this study it is reasonable to suppose that the 15°C wintertime temperatures are ecologically realistic.

The small individuals were all selected for lack of damage due to rough handling, although superficial observations may not have detected internal damage. The possibility that condition differences from post-capture feeding regimes may be irreconcilable within and between experiments will be discussed separately.

Condition

Because of holding time requirements and availability of wild fish, the red drum and spotted seatrout were retained in controlled aquaria for re-use. By extreme exercise 1 or 2 times per week these fish retained their initial performance levels and did not develop the "sluggish" performance often reported for fish in captivity. No significant differences in swimming performance were observed during intervals of up to about 3 weeks.

However, the smaller fish did seem to have relatively small metabolic scopes in some cases when compared to adult

data crudely reduced to 15°C comparison. Inasmuch as smaller fish usually grow relatively much faster than adults, it would seem logical that their metabolic scopes for activity should be larger. Because smaller fish tended to swim more slowly at an absolute rate, and because there was some erratic swimming in the groups, the indications are that these observations are not a paradox. For these smaller fish, it is suggested that the red muscle, used primarily for sustained swimming had not become fully developed. The small fish in question have only a very small amount of subcutaneous red muscle, which suggests that fatigue and not condition itself is also important in a few cases at least.

Metabolic Depression at Salinity of 30 ppt

It may be noted that for all three species of fish, the metabolic scopes at 30 ppt salinity are sometimes less than those at 40 ppt. While perhaps not statistically significant, the observations are suspicious enough to warrant further investigation. For this reason, coefficients of condition were determined for each species at each salinity (Tables 1-3). Again, the results tend not to be statistically significant due to large standard deviations of some groups of fish. This too is suspicious however and does not eliminate the possibilities (a) that some groups at 30 ppt contained fish in both good and poor condition or (b) that some groups may have had fish at 30 ppt that were differentially adapted to 30 ppt by mechanisms as yet unknown. In any event, the larger spotted seatrout at 30-35 ppt

in the study by Wohlschlag and Wakeman (1978) had a depressed scope that could be explained by poor condition.

Further investigations are underway to compare these data to other weight-length condition studies such as those used by Texas Parks and Wildlife Department personnel for their investigations of coastal marine fishes. The projected method for this evaluation is to increment the log weight of experimental fish to that predicted as average by the Texas Parks and Wildlife Department data and then to increment the metabolism by each group of fish by an equivalent amount. This procedure may eliminate any poor condition exhibited by one group of fish over another.

Schooling Behavior

Fish schools are comprised of individuals in a relatively small size range (Shaw, 1962). Breder (1965, 1976) has suggested that the largest fish in a school is no more than 15% larger than the smallest. For this reason the range of each group of artificially selected fish was calculated and expressed as a percentage of the largest fish in the group. The mean range was determined and all experiments in which the range exceeded the mean were eliminated from regression calculations. These "edited" regressions are shown in Table 7. The edited data do not change any conclusions.

While it is possible that fine variations in swimming behavior of wild fish may be associated with great variations in energy expenditure (Lindsey 1978), no great variations were observed in this study once the fish were acclimated (or

habituated) to the chamber. However, there were differences among groups, depending upon size and upon uniformity of size, in their swimming behavior. These differences are difficult to describe, and even more difficult to quantify. Furthermore, swimming behavior and associated energy expenditures do change over wide seasonal temperature ranges, and such changes undoubtedly affect juveniles differently from the subadult or larger fish.

Size and Active Metabolism

While the study under consideration involved only small fish, ordinarily classified subjectively as "juveniles", there were sufficient size ranges to indicate useful comparisons with adult responses to salinity stresses, if energy expenditures for swimming could be adequately related to size.

For adult red drum and Atlantic croaker, active and standard metabolism plus metabolic scope were calculated and adjusted to 15° directly from formulations in the Wohlschlag (1977) TWDB report. Unfortunately all the actively swimming spotted seatrout data were from 28°C from the 1976 experiments (Wohlschlag and Wakeman, 1978) so that direct extrapolation to 15°C as indicated in the results section is risky. Not only do fish swim generally more slowly at lower temperatures in winter, their metabolic responses to different salinities might well vary with temperature. (From routine metabolism data on spotted seatrout in the earlier studies on the various bays, it appears that the optimum salinity elicits a much more peaked curve of metabolic response at higher temperatures; at lower temperatures

at the same optimum, however, the routine metabolic response curve was much flatter.) The swimming velocities (X_v) for the red drum and croaker were calculated from the small fish at 15°C on the assumption that the size-standardized swimming rate $L^{0.5}s^{-1}$ should eliminate the problem resulting from the fact that the larger fish have absolute (cm s^{-1}) swimming rates higher than for small fish (Wakeman, 1978). In an attempt to verify the use of maximum swimming speeds of juveniles to predict speeds of adults, the earlier data plus the data of this study were examined in the cases of the red drum and the Atlantic croaker. The average maximum sustained swimming speed attained by adult Atlantic croaker at 15°C and 30 ppt salinity was 17.2 $L^{0.5}s^{-1}$. This was the only information at 15°C. For red drum, the closest available data was at 12°C and 30 ppt salinity. The average maximum sustained speed attained by the adults was 12.4 $L^{0.5}s^{-1}$. Red drum X_v values between 12°-28°C are nearly linear (Wohlschlag, 1977) so that maximum X_v at 15°C would be approximately 14.3 $L^{0.5}s^{-1}$. Juvenile Atlantic croaker at 15°C 30 ppt attained only 11.1 $L^{0.5}s^{-1}$ while red drum at those conditions swam at 11.3 $L^{0.5}s^{-1}$. This would indicate that our predicted active metabolic rates for the adults are too low. On the other hand, for the adult red drum, there was some indication that the $L^{0.5}s^{-1}$ increased with L.

By recalculating the active metabolism at 15°C and 30 ppt using the adult speeds, the active metabolism of the Atlantic croaker goes from 205.2 to 331.8 mg $O_2kg^{-1}hr^{-1}$ while the red drum is raised from 168.5 to 210.7 mg$O_2kg^{-1}hr^{-1}$. This is

certainly a significant change for the calculated adult Atlantic croaker. The difference in standardized maximum sustained swimming speeds may be accounted for by differences in red muscle development. It is known that the proportion of red to white muscle increases with size of fish (Magnuson, 1973). In addition it is quite possible that the shape and hyrdodynamics of a fish could change with growth (Aleyev, 1977). Thus both physiological and hydromechanical problems still exist in explaining differences in swimming performance between small and large fish.

The theoretical basis of swimming energy expenditures and observations both indicate that the smaller fish have the relatively higher drag and smaller momentum (mass times velocity). Because drag depends also on wetted surface (square of length), and to various exponents of the length and swimming velocity, it is easy to understand theoretically why energy expended to overcome drag would vary with size (Webb, 1975). The effect of size on active metabolism has received relatively little study (Brett and Groves 1979). These authors do note, however, that the log oxygen consumption rate vs. dry weight tends to increase with increasing activity and that there is a partially compensating increase in relative muscle mass with increase in size.

Species Differences Among Large and Small Fish

Feeding requirements for maintenance and growth in natural populations imply the existence of an ecological maintenance (routine) level (Brett, 1976), which must include minimal energy

for foraging (Weihs, 1973) and for assimilation of foods. For moderately active swimmers this level for swimming and/or assimilation energy expenditures is about twice the standard physiological maintenance level for fasted fish (Winberg, 1956; Mann, 1969; Kerr, 1971). To include energy requirements for growth, gonadal maturation, etc. would imply that more than ecological maintenance requirements must be met. From most types of growth theories, it should be emphasized that the relative amount of energy available for growth declines with size, but the relative amount for ecolocial maintenance and operation increases until an old fish would have virtually no energy available for growth. Further, it might be emphasized that any extra energy requirements for salinity or other stress adjustments and adaptations would more likely be available to the smaller, rapidly growing fishes (Wohlschlag and Cameron, 1967).

The ecological ranges over which a juvenile fish could maintain itself and the optimal salinities for each of the three species are discussed in the following sections.

Red Drum. Figures 1 and 3 indicate a weak peak of active metabolism at 20 ppt, with a minor depression in the standard metabolic level at the same salinity (Fig. 1). Accordingly, the scope indicates a slight optimum at this salinity. The coefficient of condition at 20 ppt was somewhat lower than the other salinities indicating that the optimum may be greater than shown. The active metabolic rate exceeds the standard metabolic rate by a factor of two over a wide salinity range; from 0 ppt to about 70 ppt. While the amount by which the

active metabolic rate exceeds twice the standard metabolic rate is never very great, this may be expected at winter temperatures.

The salinity range reported for adults in the Wohlschlag (1977) TWDB report [IAC(76-77)-1960] was 5-55 ppt indicating a broader salinity range for juveniles. Indeed, the metabolic rates in juveniles conform fairly well to Nordlie's (1978) Type I response of a fish well adapted to a euryhaline existence. The adults exhibit Nordlie's Type III response which allows freedom of movement with respect to salinity but at significant costs.

There is little published data on juveniles. Occurrences are reported by Gunter (1945) at 21-32 ppt, Schultz (1960) at 20-24 ppt and Chin (1961) at 1-33 ppt. Seining surveys by Texas Parks and Wildlife have found few red drum but that most likely is due to gear selectivity. Juvenile red drum were readily available in grass flats from April through July. The salinity at the capture sites ranged from 22 to 37 ppt and no preference was noted.

Adult red drum spawn in the Gulf of Mexico in late fall near the mouths of passes into the bay systems (Gunter 1945). Pearson (1929) indicated that conditions in the Gulf are unsuitable for the early stages following hatching. While most previous workers thought that after one year most fish leave for the deep bays and the Gulf during winter, current thought is that red drum do not generally leave the bays until age 3 (G. Matlock and T. Heffernan, personal communication).

Adjustments to the metabolic scope, as explained under the section on Atlantic croaker, do not affect the results of the experiments on red drum. The fish used at 20 ppt are somewhat emaciated but that only serves to emphasize the optimum at 20 ppt.

Atlantic Croaker. Figures 6 and 8 indicate the generally great variability in the data for the active Atlantic croaker, with no pronounced metabolic peaks at optimum salinities. The coefficient of condition at 30 ppt was significantly higher than at the other salinities, 3.6 against about 2.8-3.0. This, combined with the relatively low swimming speed and small metabolic scope at 30 ppt indicates that the fish were probably overfed and somewhat out of condition. Nevertheless the "flat" nature of the curves suggest broad euryhalinity. There does seem to be a slight peak at 20 ppt but it reoccurs at 40 ppt. If we compare our coefficients of condition with those of Parker (1971) at 3.1; Dawson (1965) at 3.15; and Avault et al. (1969) at 3.15, it would appear that the fish at 10 and 20 ppt were emaciated while the fish used at 40 ppt were in perfect condition. If we assume the fish at 40 ppt are in good condition while the fish at 10, 20 and 30 ppt are not in good condition, for whatever reason, the average actual metabolic scopes at 10, 20 and 30 ppt can be adjusted upward by a factor derived by comparing their coefficients of condition to the norm. Thus at 10 ppt $3.1/2.75 = 1.1$, at 20 ppt $3.1/2.85 = 1.1$, and at 30 ppt $3.6/3.1 = 1.2$. The results are plotted in Figure 10. There

is no experimental proof as to the validity of these data and it may well be coincidental that this method works. But in light of previous studies this method seems logical.

Whether "adjusted" data or the actual data are used, the salinity range for juvenile Atlantic croaker, i.e., when the active metabolic rate exceeds the standard metabolic rate by a factor of two, extends over all salinities normally encountered in Texas estuaries.

The adult Atlantic croaker, using limited data, showed a relatively flat curve for metabolic scope with a slight optimum at about 30 ppt and 20°C. Extrapolating to 15°C the peak occurs at 20 ppt.

The life history of the croaker is similar to that of the red drum. Spawning takes place in the fall of the year in the Gulf of Mexico off the mouths of passes into the bays (Pearson, 1928). Age I croakers do not take part in the spawning but many join the fall migration of croakers to the Gulf where they spend the winter in deeper warm waters (Pearson, 1929; Parker, 1971). Because small croakers were found in bay trawls throughout the winter, some at least winter in the deep bay waters.

References on salinity with regard to croakers are quite varied. Chin (1961) reports a peak occurrence of juveniles in Galveston Bay at 3-9 ppt with a range of occurrence from 1-21 ppt. Schlecht and McFarland (1967) found juveniles and adults at 10, 15, 20, 40 and 45 ppt salinity, while Hoese, et al. (1968) collected croakers in the Aransas Pass inlet from 24-35 ppt waters,

the normal salinity range where our fish were collected. Other sources, Pullen (1960), Mackin (1971), Hoese (1960), and James (1974), agree with this range.

Spotted seatrout. The metabolism-salinity results of Figs. 11 and 13 are more or less of the same general shape as those for adult fish. The actual data of Fig. 11 indicate the optimal salinity to be between 20-25 ppt while the calculated data, Figure 13, indicate a slightly lower optimum. It is interesting to note that minimum resting metabolism occurs at 20 ppt while maximum active metabolism is at 30 ppt.

By again determining the coefficient of condition for fish used at each salinity (Table 7), it can be seen that the spotted seatrout at 30 ppt were quite emaciated. By making the same adjustment that was made for croaker the results are changed so that the optimum would occur at 30 ppt (Fig. 15). It must be emphasized again that this method of adjustment is unproven but it has accounted for anomolies when applied thus far.

A regression which would allow extrapolation to 15°C by allowing for a decrease in maximum swimming rates with temperature was not available for adult spotted seatrout. Wakeman's (1978) results for spotted seatrout at 28°C showed optimal conditions at 20 ppt, but there was an anomaly of metabolic depression at 30 ppt.

The metabolic scope at 30 ppt was lower than that at 10, 20 or 40 ppt. This indicates that fish used in those experiments

may have been in poor condition. Available data indicate that the coefficients of condition for those fish were lower than normal (see pp 84-85 of 1976 TWDB report under (AC-76-77-0632). Moody (1949) reports occurrences of newly hatched spotted seatrout at 22-25 ppt while Schlecht and McFarland (1967) report juveniles at 4-8 and 22-27 ppt. Simmons (1957) reported occurrences of juvenile spotted seatrout in the Laguna Madre at 20-60 ppt while Gunter (1945) found juveniles at 23-25 ppt. Simmons (1957) also reported spotted seatrout spawning at 45 ppt in Laguna Madre indicating a high salinity tolerance for newly hatched spotted seatrout.

The salinity range from our experiments, when the active metabolic rate is at least twice the standard metabolic rate, is 0-55 ppt. This agrees with the above authors. Normally hypersaline waters in Laguna Madre may have caused long-term acclimatization to even higher salinities than indicated in this study.

Scope Comparisons: Species and Size. For the 15°C metabolic scope data which are pertinent for both large and small fishes, simple visual plots for each of the three species are summarized in the Fig. 18 composite. In Fig. 18A the spotted seatrout curve for adults is that extrapolated for temperature from Wohlschlag and Wakeman (1978) and for juveniles from Fig. 15 of this study. The curves are visually drawn. In a similar manner the adult and juvenile scope values from Fig. 16 for the red drum are visually drawn in Fig. 18B. Corresponding values from Fig. 17 for the Atlantic croaker are in Fig. 18C.

What these curves show is in general agreement both with their life history information for each species and with the general physiological principles associated with growth and adaptation to environmental factors like salinity. The solid part of each of the curves is based on observed data and the dashed portion on extrapolation, which may be misleading if extrapolated too far below 10 ppt and above 40 ppt salinity. The horizontal lines at a scope of 100 mg $O_2 kg^{-1} hr^{-1}$ are simply arbitrary levels that represent estimated lower operating limit for species of this family in the local Gulf coastal area. For each species the upper level for the juveniles is about what would be expected on the basis of the usual metabolism-size differential for most vertebrate species. The general spread of the lines, however, is highly characteristic of the individual species.

CONCLUSIONS

Juvenile Atlantic croaker, red drum and spotted seatrout have a generally broader and higher metabolic scope-salinity relationship than adults of the same species. The breadth (euryhalinity) of the relationships are in that order. (See Figure 18 for a diagramatic depiction of the scope relationships.)

At 15°C the optimal salinity is about 20-30 ppt for juvenile spotted seatrout and about 20 ppt for both red drum and Atlantic croaker juveniles.

On a conservative basis the scope for activity of the juveniles is much higher than the scope for adults, but the scope patterns for each of the three species are sufficiently characteristic to suggest that each species of fish would have characteristic adult and juvenile metabolic patterns and that scope measurements should not be extended from one species to another or between adults and juveniles without at least some preliminary investigations.

From these studies on juveniles and the earlier studies on adults, in which the optimum salinities for maximum scopes generally appear to be about 20 ppt and certainly not more than 30 ppt, there is an important suggestion that the entire biotic assemblage in the estuaries be examined for the same optimum salinity range, with due allowances for natural salinity fluctuations.

There is also an important implication that the same species from more brackish to fresh waters and from hypersaline

waters may respond metabolically for optimal scopes at different salinities.

For the spotted seatrout in Fig. 18A, the data for adults indicate that their scope range above 100, as an arbitrary point of departure, is much narrower than the other species with reference to salinity, while the juveniles have a somewhat broader salinity range. The red drum adults have a much broader salinity tolerance range above the 100 scope unit level in Fig. 18B, with a still broader range for the juveniles. These red drum scope-salinity depictions indicate that it can survive well from fresh waters to salinities above 45-50 ppt. Most euryhaline of all, but with a scope only slightly above the 100 level in Fig. 18C, is the Atlantic croaker. The shape and displacement of the lines indicate that the croaker is about as euryhaline as the red drum but its growth is much slower as indicated by the relative area above 100 and under the scope curves.

From the methods, results, and discussion sections above, it is obvious that a presentation like Fig. 18 could be drawn in a number of ways, especially with and without scope adjustments for condition. However, it all cases that were attempted, the juvenile sizes of all three species have the more broadly euryhaline metabolic responses. Because the smaller members of a species, once they have become truly nektonic, tend to have the broader salinity tolerance range, good water and fishery resource management practice would be obligated to adjust

operations to allow for the narrower salinity ranges required for adults. Hopefully future experiments with very large fish can extend these studies to investigate the problem of whether or not the very large fish have still narrower salinity ranges. Similarly future experiments, as well as work in progress, should indicate the nature of metabolic scope and activity relationships for fish at less than juvenile sizes in this study down to the post larval and larval stages when salinity tolerances may be very limited.

Although the present study did not examine the question in great depth, the length of time required for the juveniles and adults of the different species to become acclimatized to different salinities is still a matter that should be investigated.

The metabolic response of the juveniles at the active level particularly is inversely related to the physical condition of the juveniles in terms of their weight-length relationships (coefficient of condition). When unusually to slightly emaciated fish with considerably to slightly reduced coefficients of condition have their active metabolic rates or scopes "adjusted" upward to correspond to normal coefficients of condition, the metabolic measurements tend to be quite uniformly in agreement with metabolic results from normally healthy, vigorous fish. Apparently the juveniles of the three species are quite susceptible to weight loss--or failure to gain weight at a normal rate--when subjected to various natural and laboratory stresses, just as their active metabolic rates or scopes are

diminished with stresses.

Even with adjustments, the scope for the red drum at 30 ppt tended to be low to the extent that further studies over a 20-40 ppt range are indicated to ascertain whether this depression is an artifact or a real phenomenon associated with an ionic-osmoregulatory problem.

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